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Volume II - Octobre 1955 - Numéro 3

MASSON & C^{ie} EDITEURS - PARIS

INSECTES SOCIAUX

Revue consacrée à l'étude de la Morphologie, de la Systématique et de la Biologie des Insectes sociaux.

Publiée sous les auspices de

L'UNION INTERNATIONALE POUR L'ÉTUDE DES INSECTES SOCIAUX

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France et Union Française : **3 000 frs.**

Étranger { Dollars U. S. A. : **9,25.**
 { Francs Belges : **460.**

Également payable au cours officiel
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Prix spécial pour les membres de l'Union internationale pour l'étude des Insectes sociaux.

France et Union Française : **2 000 frs.**

Étranger { Dollars : **5,75.**
 { Francs Belges : **286.**

Règlement : a) Chèque sur Paris d'une banque officielle.
 b) Virement par banque sur compte étranger.
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POUR L'ÉTUDE DES INSECTES SOCIAUX

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TOME II

N° 3

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120, boulevard Saint-Germain, PARIS-VI^e

1955

I

MÉMOIRES ORIGINAUX

THE FIRST SOCIAL PARASITE IN THE ANT TRIBE DACETINI

by

William L. BROWN, Jr.

(Museum of Comparative Zoology, Harvard University.)

The subfamily *Myrmicinae* is, above all other subfamilies, a stock that has given rise to the most varied and most specialized kinds of social parasites. In the majority of cases, these parasitic myrmicines have obviously evolved from the same group or genus to which their respective hosts belong, and for some forms, it even seems possible that the host species itself may have been the direct ancestor of the parasite.

It is certain that parasitism has arisen many times independently among the myrmicines; the partial list below will illustrate this polyphyletic pattern. Each of the *genera* listed on the left is common, widespread, and has radiated profusely; each corresponding species listed to the right represents either a substantiated parasite or one assumed to be parasitic on the basis of good indirect evidence. Each parasite belongs to the same genus as the host, or to a genus very closely related phylogenetically.

| | |
|----------------------|--|
| <i>Myrmica</i> | <i>M. myrmecoxena</i> Forel. |
| <i>Manica</i> | <i>M. parasitica</i> Creighton. |
| <i>Pogonomyrmex</i> | <i>P. anergismus</i> Cole. |
| <i>Pheidole</i> | <i>Sympheidole elecebra</i> Wheeler. |
| <i>Aphaenogaster</i> | <i>A. tennesseensis</i> Mayr. |
| <i>Solenopsis</i> | <i>Paranamyrmex solenopsidis</i> Kusnezov. |
| <i>Monomorium</i> | <i>Epococus pergandei</i> Emery. |
| <i>Tetramorium</i> | <i>Teleutomyrmex schneideri</i> Kutter. |
| <i>Leptothorax</i> | <i>L. duloticus</i> Wesson. |
| <i>Crematogaster</i> | <i>C. ranavalonæ</i> Forel. |
| <i>Acromyrmex</i> | <i>Pseudoatta argentina</i> Gallardo. |

The majority of parasitic species is known from Europe, North Africa, North America and Argentina, suggesting that parasitism may be favored by temperate or even cold climate. However, it should be remembered that it is these very same areas where most of the intensive collecting and

biological examinations of ants have been carried out up to the present, whereas few tropical ant species have been studied at all beyond the stage of original description.

This paper is concerned with the description, and a brief discussion of the biology, of the first verified social parasite among the Dacetini—a member of the dominant and widespread genus *Strumigenys*. This is also the first verified parasite reported from among the ants of Australia, though it seems likely that at least a few of the species already known in genera such as *Monomorium*, *Crematogaster* and "*Bothriomyrmex*" may be parasites (1). Since the new species shows every evidence of being a workerless obligatory parasite on the common Australasian species *Strumigenys perplexa* (F. SMITH), of which *S. leæ* Forel is a synonym, a comparative description will be most useful. *S. perplexa* ranges widely in the moister parts of southeastern and southwestern Australia, Tasmania and the North Island of New Zealand, as well as various adjacent oceanic islands, and over most of this area it is the only, or at least the only common, member of its genus.

Strumigenys xenos sp. nov.

Holotype female, winged: TL 2,4 mm., HL 0,57 mm., ML 0,20 mm., WL 0,64 mm., CI 75, MI 35, forewing L 2,1 mm. (Measurements and their symbols correspond to those of my other papers on dacetine taxonomy; cf. Brown, 1953, *Amer. Midl. Nat.*, 50: 7-15.)

Resembling the female of *S. perplexa*, but somewhat smaller and with shorter mandibles. Also the following qualitative differences:

1. Mandibles more distinctly arcuate and slightly broader at the base, nearly twice as broad near base as at preapical tooth; tilted slightly dorsad and otherwise intermediate in general appearance between those of *S. perplexa* and the "*Labidogenys*" group of species, such as the northern Australian *S. emdeni* Forel. Apical and preapical teeth smaller and more slender than in *S. perplexa*, the preapical directed strongly obliquely apicad and nearly as long as the dorsal apical tooth.

2. Propodeal teeth and *lamellæ* weakly developed, the *lamella* subcariniform and without well-defined lower lobes or angles.

3. Spongiform appendages not so well developed; posterolateral petiolar lobes tiny, transparent; postpetiolar appendages leaf-like, transparent, and somewhat shrunken, without the abundant minute areolation and vesiculation of *perplexa* females. Anterior gastric margin with a reduced transparent border. Gastric costulation fine and close, extending about $1/4$ the length of the basal segment. Postpetiolar disc and remainder of gaster smooth and shining.

4. The pilosity consists of an even, abundant growth of fine, mostly whitish erect hairs, each weakly curved and usually with truncate apex, covering both dorsal and ventral surfaces of head and gaster, dorsum of alitrunk, nodes, legs and scapes. Hairs on funiculi, mandibles and tarsi shorter, finer, pointed, largely reclinate or appressed.

(1) The ant described as *Bothriomyrmex wilsoni* Clark, 1934, Mem. Nat. Mus. Victoria, Melbourne, 8, 39, pl. 3, fig. 5, worker, from South Australia, was supposed by its author to be a parasite of a *Crematogaster* species. From the evidence cited, the association could just as easily have been a chance or plesiobiotic one, such as I have often found under stones in South Australia and Victoria. At any rate, Clark's description and figure seem to me to fit best, not the dolichoderine *Bothriomyrmex* or its Australian counterparts, but a worker of *Plagiolepis*, of subfamily *Formicinae*. The types of *B. wilsoni* need to be checked against this surmise.

The erect hairs, which are at least three times as abundant as in *perplexa*, and longer on the average, are shortest beneath the head and longest on the gaster; in the latter position, the individual hairs are mostly longer than the greatest thickness of the posterior coxa (maximum length of hairs ca. 0.11 mm.). As seen at a magnification of 80X, the apices of the hairs are mostly blunt, or even feebly enlarged, but are not nearly so distinctly broadened as are the corresponding hairs of *perplexa*.

5. Color not very significantly different from that of *perplexa*; uniform medium ferruginous, gaster scarcely if at all darker. Head not infuscated, except for the ocellar region. Appendages lighter. Wings clear, abundantly microtrichiate; M obsolete beyond basalis; *r* distinct; Rs + M lacking, and Rs therefore basally detached, its remainder present only as a feebly pigmented furrow, not reaching wing margin. Posterior wing with a single vein near anterior margin, ending before midlength in a feeble clavation. Hamuli 4, feeble, situated beyond midlength. A small difference of doubtful importance lies with the short anteromedian mesonotal carina, which is more distinct in *xenos*, and surrounded by a feebly impressed area which forms a pit-like region at the posterior end of the carina.

The two paratypes show very little perceptible variation away from the holotype; the measurements and proportions are scarcely beyond the expected errors. In one specimen, the gastric pilosity reaches nearly 0.13 mm. in length; degree of infuscation of gaster and of ocellar triangle vary slightly among the holotype and two paratypes.

Holotype [Museum of Comparative Zoology] taken on the lower slopes of the Warburton Range, just above Warburton, Victoria; altitude about 400 M. The collection was made from a nest of *S. perplexa* in a small rotten log in a tree fern gully remnant surrounded by cleared pasture slopes, January 9, 1951 (W. L. Brown).

Paratypes: two dealate females. First paratype [South Australian Museum] taken under a stone in a nest of *S. perplexa*; wet, dark fern gully at Ferntree Gully Park, Victoria, during August, 1951 (Brown); this is the specimen upon which live nest observations were made (see below). Second paratype [destroyed in shipment] taken with one dealate *S. perplexa* female, one *perplexa* worker, and a small amount of brood, beneath a stone on the west (bay side) slope of Arthur's Seat [Mt.] at about 130 m. altitude, McCrae, Victoria, during April, 1951. This collection was made in medium rainfall sclerophyll forest, on granite (*Eucalyptus obliqua*, *E. radiata*, *E. viminalis*, *Banksia* sp.); undergrowth scanty, some grass (Brown). These localities are widely separated, and are all to the east or south of Melbourne.

BIOLOGY

This species was first detected in the collection at Arthur's Seat. This collection attracted attention because the total catch, apparently representing an incipient colony, consisted of one dealate *perplexa* female, the dealate parasite female, and one *perplexa* adult worker, plus a small amount of brood. The parasite was at first mistaken for a second *perplexa* female, but the circumstances were odd enough (for an incipient nest) to call for careful examination of each of the specimens. The unusual characteristics of the *xenos* female were apparent at once under the microscope. It being realized that I had collected only a small proportion of the many *S. perplexa* colonies seen during my Australian tour, I nevertheless examined all the alcoholic storage material of this species I had accumulated, and luckily brought to light the winged female (holotype) from the Warburton Range colony. This winged specimen was accompanied in the vial by two dealate females of *perplexa* and a number of

perplexa workers, representing only a part of the nest opened. My field notes do not indicate that more than this single winged form was seen in the nest, but my examination of the log containing the nest was recalled as a hurried one; at the time of collection, nothing unusual was expected of a colony of the common *perplexa*. None of the other *perplexa* colonies among my alcohol duplicates contained any *xenos*.

I then began an intensive search in the Dandenong Ranges, near Melbourne, and at the end of the winter in 1951, I finally succeeded in finding a single dealate *xenos* female in a *perplexa* nest consisting of 4 dealate queens and about 130 workers. The entire nest was secured alive, and with several other pure *perplexa* nests was placed under observation in glass-topped plaster chambers well provided with various live collembolans, previously found to be the prey of *perplexa*.

In the plaster nest, *S. xenos* showed markedly different behavior from the *perplexa* queens. The *perplexa* workers constantly surrounded her to the number of 3-10 at one time, and usually held her near to the brood pile. The workers were seen continually to ply their glossae over her head and alitrunk, or to hold these parts gently between the tips of their mandibles. The workers showed no signs of hostility, such as threatening or striking from the wide-open position of the mandibles, during four days of observation. When the nest was disturbed sufficiently to initiate portage of the brood by the workers, the *xenos* queen was also carried off in the mandibles of a worker (or more than one worker); for such portage, she folded her head downward and her appendages inward in a sort of pupoidal pose, rigidly held. The *perplexa* queens mostly shifted for themselves, as in pure nests, and even foraged and successfully caught collembolans on occasion; the reaction of the workers to their presence apparently was very little if any stronger than the reaction of the same workers to their worker mates. By contrast, the sedentary *xenos* female invariably drew the attention of every worker passing by her.

In observing certain other species of *Strumigenys*, I have sometimes noticed, in cases where virgin queens have accumulated to excessive numbers in exitless plaster nests, a similar kind of behavior of workers toward these females, but in such nests, the females were attended each by only a single worker, following, restraining and hauling them day and night, often for weeks at a time. The result of such maneuvers, however, was always the ejection of the females from the brood chamber, and, though the wings had always been removed previously, this may have represented a normal attempt at forcing dispersal of the females surplus to the nest. In these cases, the female has never been observed to "fold", instead, she usually seems to be trying to escape the persistent attentions of the worker in a feeble, half-hearted sort of way, and at times the worker is forced to lift her clear of the chamber floor in order to disengage her tarsal claws.

Xenos, in contrast, always attracted more than one worker at a time, and the workers appeared to be trying to get her as close to the brood as

possible. At all times, she remained quietly crouching under a mob of workers. After four days in the original host colony, the *xenos* female was removed to a pure *perplexa* colony of about 80 workers and 2 queens in a similar plaster nest. Adoption was immediately successful, and behavior of the parasite female and the new host workers was the same in all respects as it had been in the original host nest. One of the *perplexa* queens from the original nest was then transferred to the second nest, where the new workers reacted to her presence by the open-mandible threat pose, briefly held, on the first few contacts. After this, the *perplexa* queen was treated just about in the same way as were the two queens belonging to this nest, and she soon found her way to the brood and the side of these two queens. Acceptance of this foreign *perplexa* was accomplished with little difficulty, agreeing with other similar queen transfers tried with this species and with some other dacetine species. The workers of the new colony were almost indifferent to the foreign *perplexa* queen as compared to their frenzied acceptance of the *xenos* female.

It was not possible to continue observations of *xenos* in the artificial nest because of travel plans elsewhere in Australia, but the observations completed during about one week convince me that *xenos* is an obligatory and workerless parasite of *perplexa*. Unfortunately, I was unable to determine how the *xenos* female fed, or whether she laid any eggs during this period.

In no one of the three nests harboring *xenos* females could any trace of workers other than the usual *perplexa* caste be found, despite very careful checking of the latter. Females of *xenos* were never found apart from *perplexa* nests, and no workers corresponding well to the unique pilosity and other characters of the *xenos* female have ever been found in any situation. Two stray workers of a new but undescribed form allied to *perplexa* have unusually long, fine pilosity, but this does not correspond well to the pilosity of *xenos*, and the mandibular and other differences are also clear; I believe these workers have no connection with *xenos*.

The coexistence of the *xenos* and one or more *perplexa* queens in a single colony is an interesting feature of this case, and since it has been found on three separate occasions at different localities, it is hardly to be doubted that it is the usual situation. In some quarters, it has long been asserted that socially parasitized colonies could not maintain host and parasite queens for an indefinite time together. However, we now have well-studied cases available in which host queen and parasite queen (more than one parasite queen in *Teleutomyrmex*) can tolerate each other and remain together for long periods in a single colony.

Résumé.

Strumigenys xenos sp. nov. a été trouvée en Australie dans les sociétés de *Strumigenys perplexa* (F. SMITH). Sa description est faite en comparaison avec l'espèce hôte.

Il s'agit de la première espèce de Fourmi parasite connue d'Australie. Elle n'a sans doute pas d'ouvrières. Les femelles cohabitent dans le nid avec celles de l'hôte, mais sont traitées bien différemment par les ouvrières de *S. perplexa*. Tandis que celles-ci ne portent guère d'attention à leurs propres reines (guère plus qu'aux autres ouvrières), elles entourent constamment la femelle *xenos*, la lèchent, la maintiennent dans leurs mandibules, la transportent en cas de déménagement et l'entraînent le plus près possible du couvain. Transportée dans une autre société de *S. perplexa*, la femelle *xenos* est adoptée immédiatement et est l'objet du même traitement ; tandis qu'une reine *perplexa*, ainsi transportée de sa société dans une autre société de sa propre espèce, n'est acceptée qu'après une brève période d'hostilité.

Ces observations montrent que *S. xenos* est un parasite obligatoire et sans ouvrières de *S. perplexa*. L'alimentation de la femelle *xenos*, ni la ponte n'ont pu être observées.

BEE DISEASES AS FACTORS IN THE LIFE AND BEHAVIOR OF THE HONEYBEE COLONY

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The communal life of the honeybee colony is made possible by several adaptations. The normal colony has but one queen, a few hundred drones or males during the brood-rearing period, and several thousand workers. The queen is simply an animated egg-laying machine, dependent on the worker bees for her food and care. She has no mother instinct and is incapable of caring for the young or developing brood. She has no natural instinct or equipment to collect pollen or nectar, nor is she able to secrete wax or build comb. Her presence is essential for the morale of a well-balanced colony and for its survival. Her behavior in egg-laying is governed by such environmental factors as the temperature of her immediate surroundings in the hive, and by the quantity and quality of the food fed to her by the nurse bees. The more royal jelly she receives, the more she will lay within her capacity under favorable environmental conditions. She is subject to many of the diseases which affect the adults and to the over-all influence of brood diseases. Any disease that attacks the queen is highly dangerous to the colony welfare, but she is generally the last to die from other natural misfortunes which may beset the colony. The queen normally leaves the hive only on her mating flight, which may be one or more times before she begins to lay, and when her colony swarms. It is rare for a queen bee to mate after she begins to lay. She may live for two or more years during which time she imparts to the colony, through factors inherited from her own line and acquired from the sperm of the drone, all of the colony's characteristics.

The drones are the male members of the colony and serve only to assure the mating of the virgin queen. This takes place in flight, with the drone dying in the act. Since mating takes place in the air, the queen may mate with any drone flying in her immediate vicinity and not necessarily with a drone from her own hive. Drones are tolerated in the hive only as long as they are needed and while nectar and pollen are available. When they are no longer required, the workers starve them and drive them from the hive to die. Drones are subject to the diseases which affect the workers in the colony. Their length of life approximates that of the workers.

The worker bees are females without the ability to mate and therefore

are incapable of laying fertilized eggs. Workers assume the egg-laying role in hopelessly queenless colonies but produce only unfertilized eggs. They perform all of the work of the hive, engage in the various activities according to the development of their glands and the need for the different hive and field duties. These activities include cleaning the cells and the secreting beeswax and building comb, air-conditioning the hive, gathering, processing and storing nectar and pollen, scouting for water, propolis, food sources and for a new abode at swarming time, protecting the hive, and engaging in other intricate activities of their complex community life. The worker bees live for six to eight weeks during the active season of brood rearing and may live for as many months during the less active winter season.

HONEYBEES ARE SUBJECT TO DISEASES.

Honeybees, like most animals, are subject to a number of diseases that affect their individual and communal existence. The fact that bees live in closely congested colonies, in generally confined quarters, such as hives and hollow trees, and use the combs for several seasons or over a period of years, accentuates the hazards of infectious diseases. Further, since bees forage several miles from their hive for water and food sources and will resort to robbing from any available source, including honey from the combs of other colonies, certain infectious diseases are likely to be spread between colonies in any flight area.

BEE DISEASES AND THEIR CHARACTERISTICS.

Brood Diseases.

Honeybees are subject to diseases that affect not only their developing young but also the adults. The oldest recognized brood disease, called "foulbrood", was later diagnosed as two distinct diseases, American foulbrood and European foulbrood. Within the past twenty years, a third brood disease was identified and named parafoolbrood. All three are caused by distinctive bacteria and are considered as three separate diseases. The brood may also be attacked by a virus, resulting in a disease called Sacbrood, and by certain fungi, notably *Aspergillus flavus*, which also attacks adult bees under favorable conditions.

Of these brood diseases, American foulbrood, caused by *Bacillus larvae*, was considered as incurable until very recent times, and has taken a heavy toll of colonies for centuries. It attacks the different stages of larval growth but does not kill until the cell has been sealed and the larva is in the extended position on the bottom of the cell wall. The resulting scale adheres tightly to the cell wall, and under normal conditions, the bees cannot remove enough of the scales or infected larvae to keep the disease under control. When they attempt to do so, their mouthparts become

contaminated, and additional larvae are infected. The spores of this disease are the only bacteria that can survive in honey. They do not, however, affect any other organism.

European foulbrood is caused by *Bacillus pluton* and at least four other bacteria are associated with the disease, including *Bacillus alvei*, *Bacillus orpheus*, *Bacterium eurydice*, and *Streptococcus apis*. This disease generally kills the larvae while they are coiled in the bottom of the cells although in some instances many of them do not die until after their cells are sealed. The final, dried-down scales are easily removed. Colonies may simply be weakened by the disease or may be killed by it. Initial infections in a new area may cause a heavy loss of colonies. Colonies frequently recover during a nectar flow but may be so weakened as to be of little economic importance.

Parafoulbrood, while a distinct disease, has some of the gross symptoms of both American and European foulbrood. It has been serious at times in parts of Florida and an occasional infected colony has been found in other sections of the United States, including North Carolina, South Carolina, Georgia, and California.

Sacbrood is widely distributed throughout the world but seldom results in more than a slight reduction in colony strength. The colonies generally recover during a nectar flow although a few cells may be present in a susceptible colony throughout the year.

Diseases of Adult Bees.

Adult bees are subject to a number of maladies. They may be attacked by a protozoan *Nosema apis*, a mite *Acarapis woodi*, a virus causing paralysis, an amoeba *Vahlkampfia* (*Malpighamoeba*) *mellificae*, by fungi, and *Bacillus apisepcticus*, a bacterium that multiplies in the blood. Of these various adult diseases, the Acarine disease, caused by the mite, is not found in North America. Nosema disease is rather widespread and all races of bees seem to be susceptible. It seldom kills colonies but may seriously reduce their populations and cut down their productive capacity. Paralysis also occurs widely but seldom causes great economic loss. The fungous diseases and septicemia are of little importance.

Chemical and Plant Poisoning.

Complicating the symptoms of both the brood and adult diseases are the ill effects of chemical and plant poisons. The pesticides, applied for the control of insect and plant pests, are frequently destructive to honeybees in all stages and have caused heavy losses of colonies in recent years. Farmers and pest control operators have to be continually mindful of the honeybee in applying injurious chemicals to avoid causing heavy damage to the pollinators and through their destruction reducing the yields of

crops made possible or improved by the services of the bees in effecting cross-pollination.

Of the hundreds of thousands of plant species, only a few are injurious to bees through toxic elements contained in their pollen or nectar. The most important are the California buckeye (*Aesculus californica*), black nightshade (*Solanum nigrum*), death camass (*Zygadenus venenosus*), dodder (genus *Cuscuta*), leatherwood or ti-ti (*Cyrilla racemiflora*), locoweeds (genus *Astragalus*), mountain laurel (*Kalmia latifolia* western false hellebore (*Veratrum californicum*) and yellow jessamine (*Gelsemium sempervirens*).

Of these, the California buckeye, leatherwood, and the locoweeds undoubtedly cause the greatest damage. Only the honey from the mountain laurel is said to cause any indisposition in man, and it is only in a relatively small area in the Blue Ridge Mountains that this shrub occurs in sufficient quantity to produce surplus honey in favorable years. The honey is not sold for human consumption and judging from available reports is not very injurious to bees.

In addition to these various specific ailments, the adults or the brood of bees may be killed by chilling, overheating, suffocation, starvation, effects of inbreeding, and other factors.

BEE BEHAVIOR IN RELATION TO BEE DISEASES

No other insect species is subject to so many potential ailments or hazards, and yet the honeybee has survived and prospered throughout man's recorded history.

It is interesting, therefore, to try to determine how the honeybee colony can survive these numerous ill fortunes, many of which would exterminate less hardy or poorly organized insect species.

DISEASE RESISTANCE.

While all races of the honeybee, *Apis mellifera*, are subject to the same diseases, some are less susceptible or more resistant than others. Also, the ability to resist the ill effects of certain diseases appears to be an inheritable trait in most instances. This characteristic has been linked quite closely with the ability of resistant strains to "recognize" the symptoms of sick larvae at an early, probably non-infectious stage or to clean out dead or sick larvae without contaminating healthy brood or adults. It is obvious that the ability to survive is linked closely with the degree to which this ability to resist a disease is inherited.

The brood diseases result in dried-down scales which, with the exception of American foulbrood, are easily removed from the brood cells. American foulbrood is not an epidemic disease. It may become established during any part of the year when bees may contract the disease through robbing; it may also spread through the interchange of diseased equipment. The

other brood diseases usually occur during a dearth of nectar and generally decrease in intensity with the collection of a new food source which stimulates the bees to renewed activity in cleaning out the cells and in building new combs.

The beekeeping industry has to some extent helped the bees to help themselves by selective breeding to increase the resistant factors. The treatment of European foulbrood, sacbrood, and paralysis commonly includes the practice of requeening infected colonies with stock from more resistant strains. A short period of queenlessness causes a break in brood rearing and permits more bees to devote their time to eliminating the infected bees or dead larvae. The morale of a colony improves when the birth rate exceeds the death rate, and with an increase in the nectar and pollen supply, the workers prepare more cells for both brood and honey.

Since the queen is the mother of the entire colony, the artificial insemination of a queen with sperm of selected drones makes possible the intensification of various organic and behavioristic characters related to disease resistance. These characters may again be lost, or diluted, when queens mate naturally, except in very isolated situations. Natural resistance to American foulbrood has been noted in some apiaries in the Territory of Hawaii, where inbreeding is possible under natural environmental conditions because of the vast water barriers between the islands.

RESISTANCE TO EFFECTS OF CHEMICAL POISONING.

In the field of pest control, many chemicals are used that are highly toxic to honeybees. Since some species of insects have developed a resistance to certain poisons, the question is frequently asked "why hasn't the honeybee developed a resistance to various insecticides?" The house fly has developed strains resistant to DDT, but in this species, as with most other insects, every resistant female is capable of producing hundreds of other flies and thus restoring the population with resistant flies. The same is true of scale insects which are resistant to cyanide poisoning, or for thrips resistant to tartar emetic. In the honeybee, the workers engaged in field activities may be killed in the field, or they may carry poisoned pollen back to their hives, where it serves as a poison for the nurse bees and for some of the larvae. The queen is generally the last to die because her food, royal jelly, is elaborated from pollen and honey in the digestive system and the brood-food glands of the nurse bees. If any of the pollen used by the bees contains poison, it will affect the nurse bees elaborating the food and they will leave the hive to die before they can feed other bees or the queen. In this way they protect the queen from death by poisoning. Further, the nectar gatherer will die in the field if the nectar is poisoned. Should some of the field bees return to the hive with nectar that is contaminated with a pesticide, the nectar has to be taken up and processed by the hive bees to invert the sugars and to reduce

the excess moisture. The hive bees that do this work either die or leave the hive to die with the honey in their honey stomachs and so again protect their queen and the purity of the honey stored in their combs. This second or third handling of the nectar in the act of processing it into honey also tends to increase the chances of colony survival.

Some strains of the honeybee can exist in areas where the California buckeye pollen will kill other colonies. California buckeye is normally toxic in that if a sufficient amount of the toxic element in the pollen is retained in the queen's food it becomes impossible for her to lay fertile eggs. As a result, a "buckeyed" queen becomes a drone layer and if the effect is prolonged, the colony becomes depopulated and dies. Many of the workers that reach maturity during the decline of the colony are born as cripples. In the buckeye-resistant colonies, the queen retains her ability to lay either fertile or infertile eggs, a large per cent of the larvae are not affected, and relatively few bees are crippled. Just how this resistant character is acquired has not been discovered.

THE EFFECT OF CHEMOTHERAPEUTICS ON BEE BEHAVIOR.

As stated previously, American foulbrood has been considered incurable until relatively recent times. Many of our bee laws relating to the control of bee diseases are still based on this premise and thousands of infected colonies and their combs have been destroyed annually. The intensification of the natural factor of resistance to certain bee diseases was a long-range attempt to control American foulbrood other than by the compulsory destruction of the infected colonies, and combs. However, this approach was based on prevention rather than cure, and the loss of the resistant factor through natural mating habits of virgin queen bees has tended to reduce the efficiency of this method. It is still a worthwhile undertaking but one that will take many years to put in effect on a large scale.

Soon after the discovery and use of the sulfanomides in human medicine, experiments were begun to determine their influence on the growth and development of bacteria that cause the diseases of bees. Dr. Leonard Haseman of the University of Missouri published in 1945 the results of his tests in feeding sulfathiazole to colonies infected with *Bacillus larvae*, the cause of American foulbrood. He found not only that the development of the bacteria could be prevented but that the bees in an infected colony were stimulated in some way to eliminate an infection already present. Confirmations of his results prompted other investigators in different parts of the world to determine the effects of other chemicals and antibiotics on other bee diseases. The combined results have been so promising that the destructive roles of bee diseases to the beekeeping industry are gradually losing their significance, in well managed apiaries.

When an unprotected colony becomes infected with American foulbrood, the disease gradually spreads until all of the larvae are affected. The colony strength drops rapidly with the natural death of the adults

and the work of the colony is greatly disrupted. An infected colony sometimes leaves its hive as a swarm in an apparent effort to survive. Or, the remaining bees may be overcome by robber bees from other hives or even by ants. However, if the infected colony is fed with sugar syrup or dilute honey in which has been dissolved one-half gram of sodium sulfathiazole or 0.168 gram of terramycin, the medicaments inhibit the growth of the organism and enable the bees to rear healthy brood. This stimulates the bees to produce more brood food for the healthy larvae and for the queen. The queen increases her rate of laying eggs and the bees clean out more cells in the immediate brood area for the queen to lay in. The bees gradually remove the diseased material, even the tightly adhering scales of dead larvae, and clean the cells so thoroughly that healthy larvae are reared in previously contaminated cells. The work progresses as the numerical strength of the colony increases until all evidence of the disease disappears and the colony has healthy brood and a normal distribution of bees of various ages. The beekeeper can aid the bees further by reducing the size of its hive to a single set of combs, by adding more bees to aid in the hive duties, and by extracting and feeding back all of the old stores of honey after diluting and adding the required amount of sulfathiazole or terramycin. These chemicals are sometimes applied in dust or spray form and the behaviour of the bees toward the disease is the same. In all cases the chemicals in the larval food prevent the disease from developing and stimulate the adults to greater efforts in cleaning out the diseased material.

Various research workers and practical beekeepers have found that terramycin and streptomycin are effective in enabling the honeybee to overcome European foulbrood. Europeans have used different chemicals, mainly as fumigants, to combat the mite *Acarapis woodi* and thus reduce the disastrous effects of Acarine disease. Fumagillin has been used recently to reduce the incidence of the protozoan *Nosema apis* in honeybee colonies and thus to enable the bees to carry on a more normal colony behavior.

The beekeeping industry is now employing the use of therapeutics to prevent, to control and to eradicate American foulbrood as well as certain other bee diseases. The response of honeybees to the stimulating effects of these treatments has changed the concept of American foulbrood from one of utter destruction to one that envisions its ultimate control without destroying valuable colonies or equipment. It is an example of how an insect can be aided by modern medicine in its fight for survival. The place of the honeybee as an essential agent in the production of fruits, and seeds and vegetables, as well as of honey and beeswax, is more secure than ever before. Since extremely small amounts of therapeutics are needed, and since they can be administered before or after nectar-flows, the danger of contaminating honey with them is slight when they are used properly. The incidence of bee diseases in well managed apiaries is generally low and only where colonies are endangered by bee diseases, need these aids to bee behavior be used in order to maintain healthy and flourishing colonies.

Summary.

The honeybee has prospered through the years of recorded history by following a plan of life that contributes to the survival of the colony rather than to the individual. The colony is capable of air-conditioning its hive to meet changing weather and to store up food sources for adverse periods. Since it contributes to the production of fruits, seeds, vegetables and pasture crops, and produces honey, a delectable natural sweet, man has been interested in its production and care.

The honeybee is subject to many diseases which affect both the adults and the developing young. Several of the diseases have caused the death or destruction of thousands of colonies annually. Fortunately, none of these diseases are transmitted to other animals. Through the natural laws of survival, certain strains of bees have developed resistance to some of the diseases and man has assisted in this by selective breeding and cultivation of the hardier strains.

The most noteworthy contribution to the control of bee diseases has been the use of sulfathiazole, terramycin and other therapeutics in the food of bees in the spring and fall. By their use, at least one disease which had been considered as incurable for centuries can be prevented or controlled without the destruction of colonies or valuable equipment. The use of chemicals and antibiotics as therapeutic agents in disease control has measurably strengthened the position of the honeybee in our general economy and will save the beekeeping industry many thousands of dollars annually.

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THE DIVISION OF LABOUR WITHIN BUMBLEBEE COLONIES

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INTRODUCTION

In the present studies of the division of labour amongst the workers of bumblebee colonies the constancy of workers to household and foraging duties, and the constancy of foragers to the collection of nectar or pollen has been investigated. Experiments have been carried out to determine whether an individual will alter her behaviour in response to the current needs of her colony.

METHODS AND MATERIALS

Some colonies were reared in artificial domiciles in the field and in the laboratory, but the majority were collected from their natural habitat.

The relative sizes of the members of a colony was found either by weighing them individually or by recording their wing measurements. Before the members of a colony were weighed, they were confined in their nest for several hours, so that any differences between the weights of foragers and non-foragers due to variations in the amount of food in their honey-stomachs would be reduced. Bees were given individually distinctive marks. Newly emerged bees were also marked and their relative sizes recorded—usually about 24 hours after they had emerged, when they were strong enough to withstand this treatment.

Colonies were housed in observation nest-boxes. When 2 colonies were observed simultaneously, 1 serving as a control to the other, their nest-boxes were situated within a few yards of each other.

Time is recorded as G. M. T. (1).

(1) Greenwich mean time.

THE DIVISION OF THE MEMBERS OF A COLONY INTO HOUSE-BEES AND FORAGERS

The constancy of worker bumblebees to foraging and non-foraging duties.

In Table 1 bees have been classified as 'constant foragers' if they foraged on more than 70 % of the bee-days of observation, and 'constant house-bees' if they never left their nests. Most bees were either constant foragers or house-bees, but about a third of the members of any colony were inconstant to either duty. A similar division of labour even occurred between the bees of very small colonies.

TABLE 1

The constancy of worker bees to either Household or Foraging duties (includes all bees 4 or more days old)

| YEAR | COL- NO. | SPECIES | PERIOD OF OBSER- VATION (days) | MEAN PERIOD OF DAILY OBSER- VATION (hrs) | NO. OF WORKERS PER COL- ONY | CONS- TANT FORA- GERS | CONS- TANT HOUSE- BEES | INCONS- TANT FORA- GERS |
|--|-------------|------------------------|--|---|--------------------------------------|--------------------------------|---------------------------------|----------------------------------|
| 1952 | 1 | <i>B. pratorum</i> . | 3 | 4.6 | 4 | 2 | 1 | 1 <i>a</i> |
| | 2 | — | 7 | 4.3 | 3 | 1 | 1 | 1 <i>b</i> |
| | 3 | <i>B. agrorum</i> . | 4 | Irregular observa- tion. | | | | |
| | 4 | <i>B. terrestris</i> . | 12 | | 4 | 1 | 3 | 0 |
| | 16 | <i>B. sylvarum</i> . | 14 | | 10 | 4 | 5 | 1 <i>b</i> |
| | 18 | <i>B. lucorum</i> . | 15 | 2.1 | 49 | 8 | 18 | 23 |
| | 24 | <i>B. agrorum</i> . | 14 | 3.8 | 181 | 58 | 14 | 109 |
| | 24 | <i>B. agrorum</i> . | 14 | 4.6 | 31 | 7 | 19 | 5 |
| 1953 | 13 | <i>B. pratorum</i> . | 9 | 1.9 | 36 | 10 | 16 | 10 |
| <i>a</i> = queen foraged on one day only. <i>b</i> = queen foraged on first day only. | | | | | | | | |

During the period of observation of the *B. lucorum* colony (18) large numbers of queens and males emerged. The decrease in brood rearing, and the absence of young workers to take the place of dead foragers probably accounts for the relatively small proportion of non-foragers in this colony.

The date at which new workers emerged in 3 colonies was known, and it was found that the larger foragers tended first to leave their nests at an earlier age than the smaller ones—as first noted by Brian (1952).

The larger bees in each of the above colonies foraged on significantly more bee-days of observation than did the smaller ones. This result is in agreement with that of Richards (1946), Cumber (1949) and Brian (1952) who found that the mean size of the foragers of a bumblebee colony is greater than that of the house-bees. A few of the relatively large bees of colonies were never seen to forage however, and, conversely, very small bees sometimes foraged. The smaller foragers tended to forage less consistently than the larger ones (Table 2).

TABLE 2.

The relative amount of foraging undertaken by large and small foragers.

| COLONY No. | SPECIES. | PERCENTAGE FORAGERS WHO FORAGED ON OVER HALF OF THE BEE-DAYS OF OBSERVATION. | |
|------------|--------------------|--|-------------------|
| | | Below mean weight. | Above mean weight |
| 16 | <i>B. sylvarum</i> | 30 | 67 |
| 18 | <i>B. lucorum</i> | 43 | 60 |
| 24 | <i>B. agrorum</i> | 50 | 80 |

A colony was formed by confining captured foragers (*B. pratorum*) for 24 hours in a nest-box which contained brood taken from a *B. pratorum* colony. No division of labour on the basis of body size was subsequently apparent amongst the members of this colony. It was thought that those bees which undertook house-hold duties may have only comparatively recently started to forage at the time of capture.

The following experiment was carried out to determine whether there was any correlation between the length of time that a bee had performed a particular duty and her subsequent tendency to perform that duty.

On 21st May 1952 a colony was started by confining a *B. pratorum* queen and 12 captured *B. pratorum* foragers in a nest-box. On 11th June 7 more captured foragers were added to the colony, and on 13th June the entrance to the nest-box was opened so that the bees could fly. The colony was observed for short periods between 13th and 16th June. Weather conditions were bad during much of this time but 5 of the 7 bees added on 11th June foraged and collected 21 nectar loads. Nine of the original 12 bees remained alive throughout the experiment, but only 2 of them foraged and collected only 1 nectar load each. Thus, those bees which has recently been foragers foraged much more often than bees which had not foraged for some time. These results suggest that the longer an individual has been carrying out either household or foraging activities the more 'fixed' she becomes to the duty with which she has been previously concerned.

The interchange of foraging and non-foraging duties.

In August 1951 a *B. lapidarius* colony and 2 *B. agrorum* colonies were used in experiments which resulted in the loss of most of their foragers. Some of the small house-bees took their places, and the queen of the *B. lapidarius* colony also recommenced to forage.

It appeared possible, therefore, that a bee would change her occupation in response to her colony's requirements. Experiments were carried out in order to investigate this:

A.—THE REMOVAL OF FORAGERS FROM COLONIES

Colonies were observed in order to determine the occupation of each of their bees. Some, or all, of the foragers were then removed and the colonies were again observed. The results of these experiments are shown in Table 3. Several of the house-bees foraged after the normal foragers had been removed. On 10th August the foragers that had been removed were returned to Colony 29, and it was observed again 2 days later. Only 2 of the original house-bees foraged during this period—the remainder had reverted to their former duties inside their nest.

TABLE 3.

The effect on the division of labour of the removal of foragers from colonies.

| COL- ONY No. | SPECIES. | No. FORAGERS REMOVED. | BEFORE REMOVAL OF FORAGERS. | | AFTER REMOVAL OF FORAGERS. | |
|--------------------|---------------------|-----------------------------|--------------------------------|---|-------------------------------|---|
| | | | Period of observation. | No. of bees which had never foraged. | Period of observation. | No. bees foraged which had not previous- ly done so. |
| 29 | <i>B. agrorum.</i> | 24 | 14th July — 7th Aug. 1953. | 10 | 8th - 10th Aug. 1953. | 6 |
| 13 | <i>B. pratorum.</i> | 11 | 19th June — 2nd July 1953. | 11 | 2nd - 7th July 1953. | 4 <i>a</i> |
| 2 | <i>B. pratorum.</i> | 13 | 23rd - 26th June 1952. | 9 | 27th - 30th June 1952. | 6 <i>b</i> |

a = 2 recently emerged queens (and 1 bee which had not foraged since 20th June) also foraged.
b = also 2 bees which had not foraged since the 23rd June 1952.

In another experiment, a small *B. pratorum* colony containing 7 foragers was watched for 10 hours on 20th and 21st May 1952. During this time 2 foragers made twice as many foraging trips as the other 5. These

2 foragers were removed on the evening of 21st May and the colony was observed for a further 6 hours on 22nd May during which time the remaining foragers undertook 43 foraging trips as compared with a total of 22 on the previous 2 days. Foragers of a control colony foraged at an approximately constant rate during the course of the experiment.

A final experiment was performed on 2 *B. terrestris* colonies (31 & 32) in neither of which were any young bees emerging. The foragers of these colonies were captured on return to their nests and their wing lengths measured. Foragers belonging to Colony 31 were subsequently returned to their nest but foragers belonging to colony 32 were not. The sizes of foragers collected daily from Colony 32 decreased significantly more ($P < 0.02$) than foragers collected from Colony 31 (Table 4) (unfavourable weather conditions prevented foraging from July 28th until August 1st). As stated previously the house-bees of a colony are on the average smaller than the foragers. Since the removal of foragers from Colony 32 resulted in the size of the foragers that were subsequently collected becoming progressively smaller, it is highly probable that some of the original house-bees had undertaken foraging duties.

TABLE 4.

Mean wing length (mm.) of foragers of *B. terrestris* colonies. Foragers removed each day from colony 32.

| | | July. | | | August. | | |
|----------------|------|-------|------|------|---------|------|---|
| | | 26 | 27 | 28 | 1 | 2 | 3 |
| Colony 31..... | 12.9 | 13.0 | 13.0 | 11.2 | 11.9 | 12.8 | |
| Colony 32..... | 12.5 | 11.7 | 11.0 | 11.1 | 10.6 | 9.3 | |

B.—THE REMOVAL OF HOUSE-BEES FROM COLONIES

House-bees were removed from 3 colonies and observations made on the division of labour amongst the remaining bees which has previously largely confined their attentions to foraging (Table 5).

TABLE 5.

The effect on the division of labour of the removal of house-bees from colonies.

| | | | |
|--------------------------------------|---------------------|----------------------|----------------------|
| Colony No | 24 | 27 a | 27 b |
| Species | <i>B. agrorum</i> . | <i>B. pratorum</i> . | <i>B. pratorum</i> . |
| No. bees | 27 | 26 | 32 |
| No. house-bees removed | 14 | 6 | 39 |
| <i>Before removal of house-bees.</i> | | | |
| Period of observation..... | 11-19.8.52 | 26-30.6.53 | 26.6-1.7.53 |
| Ratio foragers/house-bees | 0.4 | 2.1 | 1.6 |
| <i>After removal of house-bees.</i> | | | |
| Period of observation..... | 20-21.8.52 | 1.7.53 | 2-3.7.53 |
| Ratio foragers/house-bees | 1.9 | 4.0 | 1.75 |
| <i>After return of house-bees.</i> | | | |
| Period of observation..... | 22-27.8.52 | 2-3.7.53 | 4.7.53 |
| Ratio foragers/house-bees | 0.8 * | 2.05 | 1.4 |

4 house-bees died in captivity.

Only 3 foragers of colony 24 remained inside their nest on the 2 days during which the house-bees were absent. These 3 bees had previously been inconsistent foragers and 2 of them foraged again when the house-bees had been returned. The brood of this colony consisted of 3 egg clumps, 1 small larval batch and 10 pupae. Since the reduced population present inside the nest when the original house-bees were absent was apparently adequate to perform all necessary nest duties it seems probable that before the start of the experiment more house-bees were present than the colony actually required, and that so long as sufficient food was being brought into the nest these redundant house-bees did not forage.

Colonies 27a and 27b served as controls for each other (Table 5). All except 1 house-bee were removed from colony 27a on the morning of 1st July and in the afternoon there was a large increase in the forager/house-bee ratio; only 3 bees that had previously been 'inconsistent' foragers together, with the remaining house-bee, did not forage. As in the case of colony 24 the forager/house-bee ratio decreased again soon after the house-bees were returned.

All but 1 house-bee were removed from colony 27 b on the evening of 1st July. During the next 2 days 10 bees took their place; 4 of these had foraged each previous day, and 6 had foraged on some of the days. The forager/house-bee ratio showed little change. This was probably because the individual bees had more time than in the previous experiment to adapt themselves to the changed circumstances, the forager/house-bee ratio being lower on the second day than on the first (1.2:2.3). When the house-bees were returned, 7 of the bees which had taken over house-duties foraged again.

It is thus apparent that when a dearth of house-bees occurs some of the foragers will carry out household duties.

THE DIVISION OF FORAGERS INTO NECTAR- AND POLLEN-GATHERERS

In the following investigations a forager has been classified as a pollen-gatherer if she carried a pollen load in her corbiculae when she returned to her nest, otherwise she has been assumed to be a nectar-gatherer. This assumption is justified in the vast majority of cases because:

(a) Whenever a returned forager which was not carrying pollen was observed throughout the period that she remained inside her nest between foraging trips she always deposited a load of nectar.

(b) Confirmed foragers behave in a purposeful manner when entering or leaving their nest which is not the case when they enter or leave their nest for the first time (FREE 1955 a).

(c) The lengths of the expeditions from which bees returned without loads of pollen were greater than would have been expected if they had not been foraging.

(d) Bumblebees do not necessarily leave their nests in order to defecate.

(e) Bumblebees have never been recorded collecting water.

A high percentage of the pollen-gatherers recorded had also probably collected nectar (BRIAN 1952). In the present study individual *B. sylvarum* pollen-gatherers deposited nectar as well as pollen on 19 of the 22 occasions when they were observed throughout the time between foraging trips. When a reference is made to a 'pollen load' it will be assumed that in many cases the bee concerned had also collected nectar. The term 'nectar load' will be used only when the bee concerned was not carrying any pollen.

The constancy of foragers to nectar and pollen collection.

In 1952 observations were made on 4 colonies which possessed plenty of developing brood. In these colonies relatively few foragers collected nectar only, or always pollen, throughout the entire period their colonies were observed (Table 6). With a few exceptions, notably some *B. sylvarum* pollen-gatherers, such bees were only recorded foraging for a few trips.

TABLE 6.

Constancy of foragers to the collection of loads of either nectar or pollen throughout the period for which their colonies were observed. Mean no. trips is shown in brackets.

| COLONY No. | SPECIES. | NO. DAYS OF OBSERVATION. | BEHAVIOUR OF FORAGERS. | | |
|---------------|----------------------|-----------------------------|---------------------------|--------------------------------|---|
| | | | Collected nectar only. | Always collected pollen. | Collected nectar only on some trips and pollen on others. |
| 15 | <i>B. pratorum</i> . | 10 | 14 (5.7) | 3 (1.0) | 25 (13.3) |
| 16 | <i>B. sylvarum</i> . | 14 | 4 (2.0) | 5 (45.4) | 20 (35.7) |
| 18 | <i>B. lucorum</i> . | 15 | 33 (2.9) | 16 (2.2) | 112 (13.5) |
| 24 | <i>B. agrorum</i> . | 14 | 3 (11.3) | 0 | 9 (42.5) |

The classification of bees in Table 7 as nectar- or pollen-gatherers depended upon the kind of food they collected on the greatest number of consecutive days on which they foraged. (Bees which collected nectar loads and pollen loads on an equal number of consecutive days have been included in both groups.) Individuals showed little constancy to the collection of either nectar only or always pollen on consecutive days. In general the greater number of consecutive days on which a bee foraged the less constant she was to the collection of either type of food.

TABLE 7.

Constancy of foragers to the collection of either loads of nectar or loads of pollen on consecutive days.

| COLONY No. | SPECIES. | NECTAR-GATHERERS. | | | POLLEN-GATHERERS. | | |
|------------|---------------------|-------------------|------------------------------------|---|-------------------|------------------------------------|---|
| | | No. bees. | Mean no. consecutive days foraged. | Mean no. consecutive days during which nectar only was collected. | No. bees. | Mean no. consecutive days foraged. | Mean no. consecutive days during which pollen only was collected. |
| 15 | <i>B. pratorum.</i> | 62 | 3.5 | 2.1 | 27 | 3.4 | 1.3 |
| 16 | <i>B. sylvarum.</i> | 4 | 4.25 | 2.0 | 20 | 5.2 | 4.3 |
| 18 | <i>B. lucorum.</i> | 105 | 4.4 | 2.2 | 76 | 4.2 | 1.8 |
| 24 | <i>B. agrorum.</i> | 9 | 7.3 | 3.9 | 5 | 10.0 | 3.8 |

On days when the *B. lucorum* colony (18) and *B. sylvarum* colony (16) were observed continuously for over 14 hours the proportion of pollen loads to nectar loads, which their foragers collected increased during the day. This was due to changes in the occupation of the individual bees as shown in Table 8 in which only the behaviour of bees which foraged both before and after 11.00 hours on the same day is recorded.

TABLE 8.

The change from nectar- to pollen-gathering during the day.

| COLONY | SPECIES. | DATE. | NO. OF BEES COLLECTED NECTAR ONLY. | NO. BEES COLLECTED NECTAR ONLY ON SOME TRIPS AND POLLEN ON OTHERS. | NO. BEES COLLECTED POLLEN ON EVERY TRIP. |
|--------|---------------------|---|------------------------------------|--|--|
| 18 | <i>B. lucorum.</i> | 22nd, 25th and 28th July 1952. Before 11.00 hrs. After 11.00 hrs. | 110 71 | 32 55 | 40 56 |
| 16 | <i>B. sylvarum.</i> | 29th & 31st July 1952. Before 11.00 hrs. After 11.00 hrs. | 11 1 | 7 11 | 10 16 |

During consecutive trips, however, foragers were highly constant to the collection of either loads of nectar or pollen (Table 9). The number of consecutive trips from which a forager returned with either loads of

nectar or pollen increased directly with the total number of loads of nectar or pollen which she collected during the course of an observation period. Thus, during relatively short periods many foragers were constant to the collection of one or other type of food, but over longer periods they showed little constancy.

TABLE 9.

Constancy of foragers to the collection of either loads of nectar or loads of pollen on consecutive trips.

| COLONY No. | SPECIES. | NECTAR-GATHERERS. | | | POLLEN-GATHERERS. | | |
|------------|----------------------|-------------------|---|--|-------------------|--|---|
| | | No. bees. | Mean no. trips per observation period during which nectar only was collected. | Mean no. consecutive trips during which nectar only was collected. | No. bees. | Mean no. trips per observation period during which pollen was collected. | Mean no. consecutive trips during which pollen was collected. |
| 15 | <i>B. pratorum</i> . | 100 | 3.8 | 3.6 | 62 | 3.9 | 3.6 |
| 16 | <i>B. sylvarum</i> . | 40 | 4.8 | 4.6 | 89 | 6.3 | 6.0 |
| 18 | <i>B. lucorum</i> . | 157 | 4.9 | 4.3 | 105 | 3.5 | 3.2 |
| 24 | <i>B. agrorum</i> . | 60 | 5.2 | 5.0 | 56 | 4.1 | 4.0 |

The relationship between the size of a bee and pollen collection.

Brian (1952) found that the larger foragers of *B. agrorum* colonies tended to collect a significantly greater proportion of pollen loads to nectar loads than did smaller foragers. In the present work this has also been found to be true in the case of colonies of *B. agrorum*, *B. lucorum*, *B. pratorum*, *B. sylvarum* and *B. terrestris*. However, even very small foragers of these colonies did collect some pollen.

The sequence of foraging duties with age.

Whether or not bees belonging to colonies 16 and 18 collected nectar or pollen during their first day of foraging was recorded. A significantly greater ($P < 0.01$) number of young foragers from colony 18 (*B. lucorum*) collected nectar loads only rather than pollen loads (36: 8). The ratio of nectar to pollen loads collected by these bees during their first few days of foraging was significantly higher ($P < 0.001$) than that of the older bees of the colony during the same period. Twenty-five young

queens of this colony collected nectar only on their first day of foraging although later some of them collected pollen.

In the case of the *B. sylvarum* colony, however, 11 out of 13 bees collected pollen on their first day of foraging.

***The relationship between the presence of larvæ in a colony
and the collection of pollen by its foragers.***

In April 1952 a *B. terrestris* queen was found to have occupied an artificial domicile. On 5th May her brood was in the larval stage and pollen loads had been deposited around it. On 14th and 15th May, by which time the larvae had pupated, the queen was seen to return to her nest 13 times, but on no occasion did she carry pollen although conditions were suitable for its collection, presumably because she no longer had larvae to feed.

Colonies of *B. pratorum* were used in the first experiment. The brood of colony 1 consisted of a group of old larvae, some of which had already spun their cocoons, and a group of young larvae. The young larvae were removed on May 18th 1952 by which time all the older larvae had pupated. During observations on 20th, 21st and 22nd May the foragers of this colony collected *111 nectar loads* but *no pollen loads*. During the same period the foragers of the control colony (colony 2) which contained a single batch of larvae, collected *16 nectar loads* and *8 pollen loads*. Further observations were made on these 2 colonies on 26th and 27th May by which time colony 1 again possessed larvae and Colony 2 contained no larvae, its former larvae having pupated. During these observations bees from Colony 1 collected *37 nectar loads* and *21 pollen loads* and foragers of colony 2 collected *9 nectar loads* and *no pollen loads*.

The presence of larvae in a colony therefore had a highly significant effect ($P < 0.001$) on the relative proportion of pollen to nectar loads which its foragers collected.

In the second experiment a *B. lucorum* colony was divided into 2 parts A and B, of approximately 40 bees each. Both parts contained pupae but, whereas colony A contained larvae and a queen, colony B did not. On 14th and 15th August the foragers of Colony A collected *14 nectar loads* and *15 pollen loads* and the foragers of colony B collected *19 nectar loads* but *no pollen loads*.

On the evening of 15 August the worker bees of colony A were interchanged with those of colony B and the positions of the nest-boxes were also interchanged so that the bees continued to forage from a nest-box in the same position as before but each colony contained the others' brood. During observations on 16th and 18th August the bees of colony A (which was now without larvae) collected *19 nectar loads* and *1 pollen load* and the bees of colony B collected *8 nectar loads* and *2 pollen loads*. The collection of pollen by foragers was thus again related to the presence of larvae in their colonies (Degree of significance $P < 0.02$).

TABLE 10.
Number of nectar and pollen loads collected by foragers of *B. agrorum* colonies with and without larvæ.

| PERIOD OF OBSERVATION. | | COLONY 29. | | COLONY 33. | | |
|---|--------------------------------|----------------------|---------|----------------------|---------|--|
| | | No. loads collected. | | No. loads collected. | | |
| | | Nectar. | Pollen. | Nectar. | Pollen. | |
| 15th, 16th & 17th (a. m.) July 1953. | Larvæ in both colonies. | 29 | 34 | 27 | 53 | Relative increase in nectar collection by colony 29. $P < 0.05$. Relative decrease in pollen collection by colony 29. $P < 0.01$. |
| | Larvæ absent in colony 29. | 69 | 23 | 29 | 103 | |
| 19th, 20th & 21st July 1953. 22nd, 23rd, & 24th July 1953. | Larvæ absent in colony 29. | 57 | 14 | 70 | 87 | Relative increase in nectar collection by colony 33. $P < 0.5$. Relative decrease in pollen collection by colony 33. $P < 0.5$. |
| | Larvæ absent in both colonies. | 83 | 7 | 124 | 23 | |
| 1st, 2nd & 4th August 1953. 5th & 6th August 1953. | Larvæ in both colonies. | 77 | 30 | 55 | 60 | Relative increase in nectar collection by colony 33. $P < 0.05$. Relative decrease in pollen collection by colony 33. $P < 0.01$. |
| | Larvæ absent in colony 33. | 54 | 30 | 69 | 22 | |

Two *B. agrorum* colonies both of which contained plenty of larvae were used in the third experiment (Table 10). The removal of larvae on 17th July and on 4th August resulted in the foragers of the experimental colony collecting relatively fewer pollen loads and relatively more nectar loads in comparison with those collected by the foragers of the control colony.

In contrast to the behaviour of pollen-gatherers of pollen-storing species (e.g. *B. lucorum*, *B. pratorum*, *B. terrestris*) which deposit pollen in storage cells, the foragers of *B. agrorum* colonies (pocket-making species) deposit pollen directly into pockets attached to larval groups (Sladen 1912).

When no larval pockets were available pollen-gatherers of colony 29 deposited their pollen loads in empty cocoon cells but the members of colony 33 constructed a tall cylindrical wax cup in which they stored pollen just inside the nest entrance. This cup was later destroyed and a similar one built near to the centre of the nest. Some pollen loads were still deposited in it even when larval pockets again became available.

The requirements of colonies in relation to their stores of food.

A study has been made of the requirements of colonies (as revealed by their foraging activities) in relation to their stores of food.

A. — THE EFFECTS OF ADDING SUGAR SYRUP TO THE FOOD STORES OF COLONIES

In 5 experiments half of the honey-pots of small *B. pratorum* colonies were filled with sugar syrup. The foragers of these colonies were observed to collect 12 pollen loads and 87 nectar loads before the addition of the syrup, and 14 pollen loads but only 6 nectar loads afterwards. During the same 2 observation periods, the foragers of 5 control colonies collected 3 pollen and 94 nectar loads, and 13 pollen and 74 nectar loads respectively. Thus the addition of sugar syrup to the experimental colonies resulted in their foragers collecting relatively less nectar than previously (Degree of significance. $P < 0.001$).

Only 4 of 26 nectar-gatherers which returned to the experimental colony after syrup had been added to their food stores foraged again, whereas 22 of 25 nectar-gatherers which returned to the control colonies during the same period continued to forage (degree of significance. $P < 0.001$).

There was no significant difference between the relative numbers of pollen-gatherers of the experimental and control colonies which remained in their nests or foraged again.

Similar experiments were carried out with 2 large *B. terrestris* colonies. (Table 11). On each of 3 occasions that sugar syrup was added to 1 or

other of these colonies its foragers collected significantly fewer ($P < 0.001$) nectar loads than previously. Only in the first experiment did the addition of sugar syrup to a colony result in its foragers collecting relatively more pollen. The carbohydrate stores of this colony (No. 31) were previously very low and it seems probable that its foragers only collected pollen when the carbohydrate stores had reached a certain minimum level (which condition was attained after the addition of sugar syrup by the experimenter).

TABLE 11.

The effect on the no. of nectar and pollen loads collected of adding sugar syrup to the food stores of colonies of *B. terrestris*.

| PERIOD OF OBSERVATION. | | COLONY 31. | | COLONY 32. | |
|---|------------------------------|----------------------|---------|----------------------|---------|
| | | No. loads collected. | | No. loads collected. | |
| | | Nectar. | Pollen. | Nectar. | Pollen. |
| 10th, 11th & 13th (a. m.) July 1953. | Syrup added to colony 31. | 269 | 0 | 125 | 169 |
| 13th (p. m.) 14th & 15th July 1953. | | 235 | 93 | 276 | 473 |
| 14th, 15th & 16th July. | Syrup added to colony 31. | 326 | 173 | 217 | 353 |
| 17th, 18th & 19th July. | | 120 | 181 | 281 | 341 |
| 18th, 20th & 21st July. | Syrup added to colony 32. | 133 | 215 | 252 | 303 |
| 23rd, 24th & 25th July. | | 220 | 179 | 196 | 118 |

B.—THE EFFECTS OF ADDING POLLEN TO THE FOOD STORES OF COLONIES

In 4 experiments the pollen stores of colonies were artificially supplemented with fresh pollen (trapped from a honeybee colony). All of these colonies contained plenty of developing brood. The results are shown in Table 12.

Experiment 1 was performed on small *B. pratorum* colonies. Four

TABLE 12.

The effect on the number of nectar and pollen loads collected of adding pollen to the food stores of colonies.

| EXPERIMENT No. | SPECIES. | BEFORE THE ADDITION OF POLLEN. | | | | AFTER THE ADDITION OF POLLEN. | | | |
|----------------|---|--|------------------------------|------------------|---------|---------------------------------|------------------------------|------------------|---------|
| | | Date. | Period of observation (hrs). | Loads collected. | | Date. | Period of observation (hrs). | Loads collected. | |
| | | | | Nectar. | Pollen. | | | Nectar. | Pollen. |
| 1 | <i>B. pratorum</i> . " | 3rd June 1952. | 4.5 | 3 | 10 | 4th June 1952. | 5.0 | 4 | 2 |
| | | | | 28 | 1 | | | 19 | 4 |
| 2 | <i>B. pratorum</i> . " | 19th, 20th, & 22nd, 23rd (a. m.) July 1953. | 5.5 | 28 | 41 | 23rd (p. m.) 25th June 1953. | 6.5 | 75 | 30 |
| | | | | 30 | 19 | | | 45 | 32 |
| 3 | <i>B. agrorum</i> . " | 17th, 18th, & 19th Aug. 1953. | 8.0 | 70 | 54 | 20th, 21st & 22nd Aug. 1953. | 9.0 | 116 | 0 |
| | | | | 84 | 30 | | | 66 | 16 |
| 4 | <i>B. terrestris</i> . <i>B. lucorum</i> . | 17th, 18th & 19th Aug. 1953. | 8.0 | 214 | 68 | 20th, 21st & 22nd Aug. 1953. | 8.5 | 274 | 40 |
| | | | | 76 | 9 | | | 103 | 5 |

empty cocoon cells of Colony 1, 2 of which had been used for pollen storage, were filled with pollen. The foragers of this colony subsequently collected relatively less pollen than previously. (Degree of significance, $P < 0.05$).

Two larger *B. pratorum* colonies were used in the second experiment. After the addition of plenty of pollen to colony 13 its members also collected comparatively less pollen than previously (Degree of significance, $P < 0.05$). However, the change was gradual and no immediate effect was observed.

Colonies of *B. agrorum* were used in Experiment 3. Six balls of pollen, each about 1.0 mm in diameter, were given to colony 39. None of the foragers of this colony collected pollen during the next 3 days of observation, but foragers of the control colony (40) still collected pollen, although at a reduced rate. (Degree of significance, $P < 0.001$). This result was surprising, since *B. agrorum* pollen-gatherers normally deposit pollen directly into larval pockets (as previously described) and it indicated that either the workers of colony 39 had transferred the pollen to the larval pockets with their mandibles or else had fed the larvae with regurgitated food. After the addition of pollen to Colony 29, 21 of the original pollen-gatherers collected nectar, as a result of which this colony showed a comparative increase in the number of nectar loads collected ($P < 0.01$).

In the final experiment pollen was added to a *B. terrestris* colony (42). Unfortunately a proper control was not available and a *B. lucorum* colony (43) which did not contain larvae had to serve this purpose. The foragers of colony 42 collected a smaller proportion of pollen to nectar loads than before the pollen was added, but pollen collection by members of the control colony also decreased and no significant result was obtained.

From the above data it appeared that pollen collection by foragers is voluntary rather than obligatory. In order to verify this a *B. agrorum* colony was placed beside a small patch of red clover and whilst one observer recorded the foragers when they returned to their nest another confirmed their presence on the crop. It was found that during the same period some of these foragers collected nectar only whilst others collected pollen.

DISCUSSION AND CONCLUSIONS

Cumber (1949) suggested that the smaller workers of a humblebee colony forage when their colony is dying out. Brian (1952) found that house-bees began to forage at about the time of the death of some of the original foragers. In order to determine whether house-bees would alter their behaviour in response to their colony's needs she took away the foragers and gave sugar syrup to a *B. agrorum* colony. The sugar syrup was removed from this colony after 28 hours during which time 1 house-bee had foraged; the next day no house-bees were observed to leave their nest.

The results of 5 experiments, in the present work, in which foragers were removed from their colonies show conclusively that some house-bees will forage in their absence. When these results are considered in conjunction with those of Brian it appears probable that house-bees only forage when the food stores of their colony become low, and that they take some time to adjust themselves to the new conditions. Some foragers also remained inside their nests when the house-bees of colonies were moved, although many of the foragers did not immediately adapt themselves to the changed circumstances. Free (1955b & 1955c) found that foragers which were confined in nest-boxes and provided with ample food laid eggs and 'nursed' the resultant larvae. It is thus apparent that although the majority of the bees of a colony are consistent foragers or consistent house-bees, many will perform either task in accordance with the current requirements of their colony.

In large colonies some bees alternate their household and foraging activities with guard duty at the nest entrance.

Sladen (1912) and Brian (1952) noted that some of the foragers of *B. agrorum* colonies collected pollen when there were no larvae in their nests. In the experiments described above a correlation has been found between the amount of pollen collected by foragers and the presence or absence of larvae. It appears that the presence of larvae releases the pollen collecting behaviour of foragers, although some of them continued to collect pollen after all the larvae have been removed from their nests.

Sladen (1912) found that when he gave food to colonies it tended to make the workers "lazy". Brian (1952) reported that by filling the honeypots of a colony with sugar syrup she induced the foragers to remain inside their nest. During the present observations when sugar syrup was added to the stores of colonies the pollen-gatherers continued to forage, but the majority of the nectar-gatherers ceased to forage for nectar and did not undertake pollen collection instead. These results further illustrate the constancy of foragers to the collection of either nectar or pollen loads throughout relatively short periods.

On most occasions when the pollen stores of colonies were artificially increased relatively less pollen, and in the case of a *B. agrorum* colony relatively more nectar, was collected. The removal of larvae from *B. agrorum* colonies also resulted in increased nectar collection.

From these results it is apparent that the type of food collected is determined to some extent by colony requirements. These requirements depend on the nature and amount of the food stores in a colony and on the age of the brood. Fluctuations in these factors, and in pollen availability in the field, can explain the day to day variations in the kind of food collected by individual foragers.

Summary.

1. Most of the workers of a bumblebee colony are either consistent foragers or house-bees but about a third of the workers are inconsistent to either duty. The longer a worker has been carrying out either household or foraging duties the more 'fixed' it becomes to the duty concerned.
2. Individual workers will change their occupation and perform either household or foraging duties in accordance with the current requirements of their colonies.
3. Foragers show great constancy to the collection of either pollen loads or nectar loads during consecutive trips, but they show little constancy for periods of a day or over.
4. The amount of pollen which the foragers of a colony collect is related to the presence of larvae in their nest.
5. The type of food collected by foragers is also determined to some extent by the nature of their colonies' food-stores.

Résumé.

1. Les ouvriers d'une colonie de bourdons se divisent pour la plupart en deux catégories bien définies, les récolteurs et les travailleurs au nid ; toutefois ils peuvent, pour un tiers, passer d'une catégorie dans l'autre. Ils se spécialisent d'autant plus dans l'une ou l'autre de ces fonctions (travail au nid ou de récolte) qu'ils les assument plus longtemps.
 2. Pris séparément, chaque ouvrier change d'occupation et passe du travail au nid à celui de la récolte, ou vice-versa, selon les besoins du moment de la colonie.
 3. Pour la durée de quelques voyages consécutifs, les récolteurs se montrent très assidus dans leur recherche, soit de pollen soit de nectar, mais pour de plus longues durées (un jour entier ou plus) ils se montrent très changeants.
 4. La quantité de pollen que les récolteurs de la colonie recueillent est proportionnelle au nombre des larves du nid.
 5. De plus, le genre de nourriture amassée par les récolteurs dépend, dans une certaine mesure, de la nature des provisions de la colonie.
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LA FONDATION DE NOUVELLES SOCIÉTÉS PAR *BELlicosITERMES NATALENSIS* Hav.

par

Pierre-P. GRASSÉ et Ch. NOIROT

Nous savons en gros comment sont fondées les sociétés des Termitidæ, mais le détail des phénomènes reste à préciser. La fondation des termitières de Macrotermitinæ est particulièrement mal connue ; c'est regrettable, car elle est plus complexe que toute autre à cause de la construction d'une meule à champignons. Quelques maigres données ont été fournies par HARMS (1927) et par LÜSCHER (1951). Divers renseignements ont été publiés par l'un de nous dans l'article « Isoptera » du *Traité de Zoologie* (1949).

Dans la présente note, nous exposons certaines de nos observations relatives à la fondation du nid chez *Bellicositermes natalensis* de Côte d'Ivoire (Adiopodoumé) et de Haute-Guinée (N'Zo, au pied du mont Nimba).

Des couples sont constitués avec des imagos ailés pris à la lampe, le 27 mars (N'Zo) et le 6 avril (Adiopodoumé), entre 20 heures et 21 heures ; ils sont placés dans des tubes d'élevage dont la figure 1 indique la structure ; insistons sur le fait que ceux-ci ne contiennent alors aucune trace de bois ou de toute autre substance alimentaire.

Ces couples n'ont pas effectué la promenade nuptiale rituelle ; mais nous savons que, chez *Calotermes flavicollis*, *Reticulitermes lucifugus* et *R. lucifugus santonensis*, la fondation du nid opérée à l'aide d'imagos prélevés directement dans le nid se déroule normalement, à condition que les imagos soient physiologiquement mûrs (GRASSÉ, 1942). Comme nos sujets ont participé au vol d'essaimage, ils sont dans des conditions moins anormales que les imagos des *Calotermes* et *Reticulitermes* pris au nid et, *a fortiori*, doivent manifester un comportement normal ou presque.

Les imagos se débarrassent très rapidement de leurs ailes et s'enfoncent dans le sol au cours de la nuit ; arrivés à une profondeur de 20 centimètres environ, ils creusent une chambre qui, en largeur, mesure à peu près le diamètre du tube et, en hauteur, une trentaine de millimètres. Cette cavité est le copularium (nous n'avons pas observé le coït). Les premiers œufs sont vus quinze jours plus tard. Peut-être la ponte commença-t-elle plus tôt, mais, les sexués ayant revêtu les parois de verre d'une couche d'argile, l'observation était difficile ; les œufs ne pouvaient être vus que par les quelques points du verre laissés nus par les Insectes. Dans certains cas, la

totalité de la paroi du tube étant tapissée d'argile, l'observation devenait impossible.

La première larve éclôt le 46^e jour suivant la fondation. Le 49^e jour, tous nos élevages contenaient quatre larves. Le premier *petit soldat-blanc* est vu le 60^e jour ; les larves étaient alors nombreuses, mais leur numération exacte n'a pu être faite à cause de l'écran d'argile. Le 68^e jour, on observe dans tous les tubes un ou deux petits ouvriers.

Dès que la présence de petits ouvriers est constatée, des fragments de bois sont introduits dans la terre surmontant le copularium.

Au 76^e jour apparaît le premier petit soldat parfait. Au 84^e jour, dans l'un des tubes, trois petits soldats sont visibles (peut-être y en avait-il davantage).

A ce moment, toute la population est confinée dans le copularium, resté dans l'état où le roi et la reine l'avaient creusé ; autrement dit, absence totale de constructions en terre et de meule à champignons.

Entre le 88^e et le 95^e jour suivant la fondation, les petits ouvriers, déjà nombreux, creusent à partir du copularium une galerie ascendante qui aboutit aux fragments de bois. Peu après apparaissent les premiers grands ouvriers.

Les fragments de bois déposés à la surface de la terre contenue dans le tube et un peu enfoncés dans celle-ci sont attaqués par les ouvriers qui ont construit des galeries couvertes à la surface libre desdits fragments de bois.

Les ouvriers, selon les colonies, bâtissent l'*habitacle* 95, 98 ou 100 jours après la fondation. A ce moment, l'*habitacle* n'est pas distinct de la cellule royale. Il est maçonné en terre argileuse et entièrement contenu dans le copularium ; il laisse un espace libre entre lui et la paroi du tube d'élevage. Il affecte la forme d'une noix et mesure environ 30 millimètres de haut sur 20-25 millimètres de plus grande largeur. Sa paroi a environ un millimètre d'épaisseur ; elle est lisse sur sa face interne et légèrement grenue sur sa face externe. A son pôle supérieur, elle est percée d'un unique orifice circulaire de 2^{mm},5, trop petit pour livrer passage aux sexués. L'*habitacle* est fixé aux parois du tube par des saillies peu nombreuses, en mamelons bien isolés. Dans un cas, l'*habitacle* fut fixé directement à la paroi de verre, sur une surface assez grande pour qu'il fût possible, pendant un certain temps, de voir les Termites dans leur logis.

Nous avons été très frappés par la rapidité avec laquelle les ouvriers construisent l'*habitacle* ; une nuit leur suffit pour achever leur tâche. *Aucune ébauche* ne précède cette construction, qui, d'emblée, aboutit à un édifice complet. Le caractère spontané de ce travail mérite d'être mis en valeur. Toutefois, rappelons qu'il est précédé de peu par le forage des galeries ascendantes dans le sable argileux et de galeries couvertes au niveau du bois servant d'aliment.

La construction de l'*habitacle* a pour effet de diviser l'espace du copularium en deux : un espace qui est la cavité même de l'*habitacle* et un espace qui règne entre celui-ci et les parois du copularium. Si on se réfère à nos travaux antérieurs (GRASSÉ, 1944, GRASSÉ et NOIROT, 1949 et 1951), on

homologuera la cavité de l'habitacle à l'*endoécie* et l'espace compris entre la paroi de l'habitacle et la paroi du copularium à la *paraécie*. Quant à la paroi de l'habitacle, elle correspond à l'*idiothèque*, telle que nous

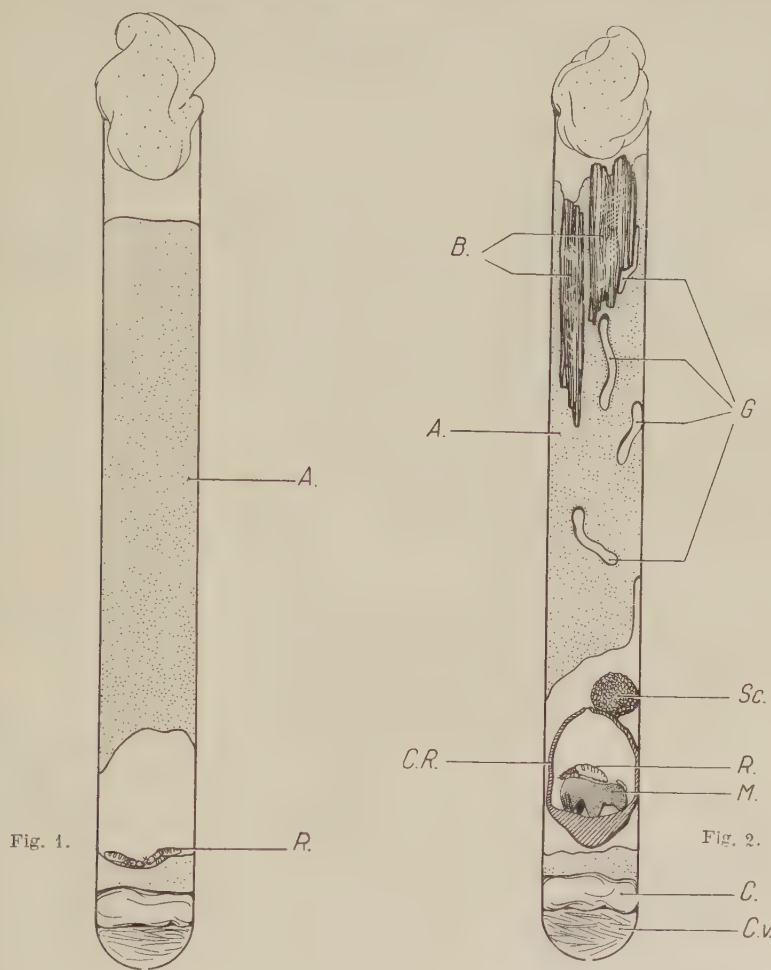


Fig. 1 et 2. — Les constructions de la jeune colonie dans les tubes d'élevage ($\times 1/2$). 1 : vers le 30^e jour ; 2 : vers le 105^e jour. A, argile ; B, bois ; C, coton ; C. R., paroi de l'habitacle, délimitant la cellule royale = *idiothèque* ; C. v., coton de verre ; G, galeries ascendantes creusées par les ouvriers ; M, meule à champignons ; R, sexués fondateurs ; Sc, amas de sciure de bois.

l'avons définie en 1951. Les galeries verticales conduisant aux fragments de bois sont tout naturellement l'amorce de la *périécie*.

Trois jours après la construction, on aperçoit, reposant sur le haut de l'habitacle, un amas de sciure de bois, grossièrement sphérique, de la taille d'un gros pois ; il est de couleur blanc-jaunâtre et fait de débris ligneux grossiers (Sc, fig. 2).

Dans l'unique tube d'élevage où l'intérieur de l'habitacle restait visible,

nous avons observé, le dixième jour suivant la construction de l'habitacle, *une meule à champignons*, un peu plus grosse que l'amas de sciure, ressemblant à une petite bille. Assez compacte, elle portait déjà quelques mycotêtes fort petites ; la présence de celles-ci permet de supposer que la meule avait été confectionnée quelques jours plus tôt. La meule est sûrement l'œuvre des ouvriers, *seuls* à sortir de l'habitacle pour récolter le bois nécessaire à sa construction.

Des observations nous ont appris que les amas de sciure sont utilisés par les habitants. Nous les avons vus disparaître, notamment dans un cas où le bois mis à la disposition de la société s'altérait ; en redonnant du bois sain à ladite société, un nouvel amas de sciure apparut au-dessus de l'habitacle. La localisation de la sciure au sommet de l'habitacle n'est pas un fait constant. Une société, transférée de son tube d'élevage à l'intérieur d'un bocal, plaça les boules de sciure *au-dessous* de l'habitacle.

Nos observations laissent encore sans réponse la question de l'origine des champignons qui poussent sur les meules. Nous n'avons jamais pu voir l'un des sexués fondateurs « fécondant » la meule de ses excréments comme le fait la femelle fondatrice des Fourmis *Attini*.

Si, dans le contenu intestinal des essaimage, on trouve fréquemment et en abondance des spores de champignons (GRASSÉ, 1944 ; NOIROT, 1952), il est malaisé d'affirmer que celles-ci proviennent bien des mycotêtes. Le problème reste ouvert.

Entre nos colonies expérimentales à habitacle non cloisonné et les jeunes termitières encore entièrement hypogées décrites par l'un de nous (GRASSÉ, 1944), les stades intermédiaires nous manquent.

Nous avons eu cependant des habitacles dont le fond était très épais et le plancher horizontal ; ne s'agit-il pas alors de l'ébauche du socle qui s'observe dans les termitières plus âgées ? C'est possible, mais non certain.

Au bout de quatre mois et demi, les colonies, devenues trop populeuses (dépassant 50 individus), furent introduites dans des bocal ; ce transfert ne fut guère favorable aux jeunes sociétés qui, quatre à cinq mois plus tard, périrent après avoir reconstruit un nouvel habitacle. Il nous paraît que le moment où le couple royal, ayant épuisé ses réserves, doit être nourri par les ouvriers est une épreuve redoutable pour la jeune société qui, même dans la nature, ne la surmonte pas facilement.

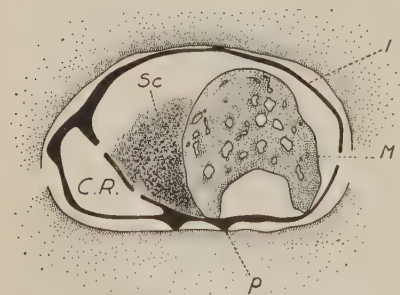


Fig. 3. — Très jeune termitière d'*Acanthotermes acanthothorax* vue en coupe ($\times 1$) [d'après GRASSÉ et NOIROT, 1951]. C. R., cellule royale ; I, idiotheque à l'extérieur de laquelle s'étend la paraécie ; M, meule à champignons ; P, piliers ; Sc, sciure de bois.

Les termitières encore entièrement souterraines de *Bellicositermes natalensis* portent la marque de leur origine. Leur habitacle, en dépit de sa

grande taille, a une enveloppe continue, percée çà et là d'orifices qui le mettent en communication avec un espace périphérique, lequel résulte manifestement de l'agrandissement de la paraécie primitive (fig. 4).

La termitière d'*Acanthotermes acanthothorax* ne dépasse pas ce stade d'organisation, tout en conservant la possibilité de s'accroître. Nous avons eu la bonne fortune de trouver une toute jeune colonie de cette espèce avec un habitacle cloisonné (fig. 3, GRASSÉ et NOIROT, 1951) dont un

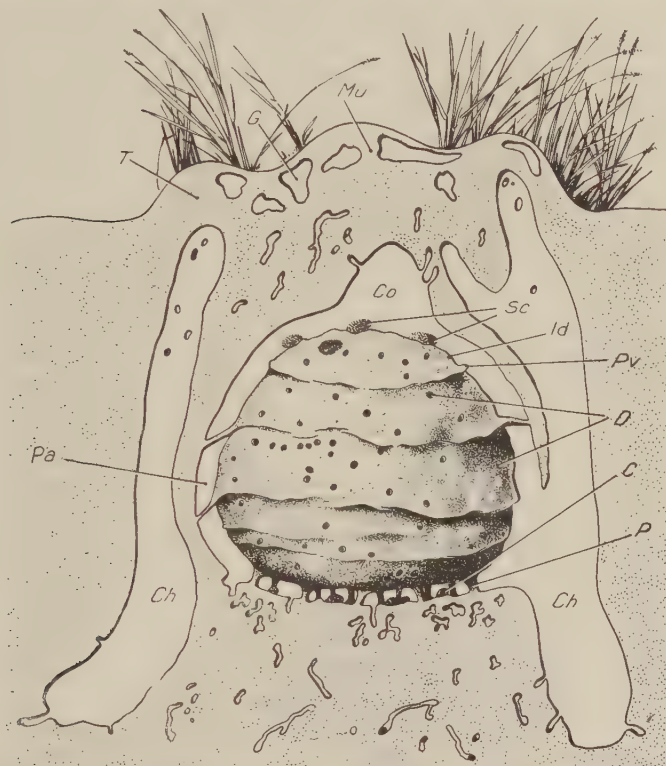


Fig. 4. — Jeune termitière, encore souterraine, de *Bellicositermes natalensis* (d'après GRASSÉ, 1944).

C, cailloux ; Ch, cheminées ; Co, coupole surmontant l'habitacle ; Id, idiothèque ; O, orifices de l'idiothèque faisant communiquer l'habitacle avec la paraécie ; P, piliers supportant l'habitacle ; Pa, paraécie ; Pv, « plis en volant » ; Sc, amas de sciure de bois ; T, amorce des tourelles.

des compartiments servait de cellule royale et l'autre contenait la première meule à champignons et un amas de sciure de bois ; cet état marque le début du découpage en chambres de l'habitacle définitif. Ultérieurement, chez *Bellicositermes natalensis*, la surrection du nid aboutit à la confusion de la paraécie et de l'endoécie, surtout par « éclatement » de la paroi limitant l'habitacle ; le nid âgé de *Bellicositermes natalensis* ne possède plus d'idiothèque reconnaissable. Disons encore que le nid de l'*Acanthotermes* a toujours une idiothèque et que celui de *Macrotermes mülleri* la conserve en partie au stade « adulte » (GRASSÉ et NOIROT, 1951).

En fait, nous confirmons sur de nouveaux documents que, parmi les

Macrotermitinae, un ensemble de genres (*Acanthotermes*, *Macrotermes*, *Bellicositermes*) se caractérisent par la construction d'un habitacle ayant une paroi propre, l'idiOTHÈQUE. Il est vraisemblable que *Sphaerotermes* a, lui aussi, un habitacle à idiOTHÈQUE, mais celle-ci s'épaissit, se complique et forme la muraille d'une calie.

La littérature scientifique est pauvre en documents relatifs à la fondation de nouvelles colonies par les Macrotermitinae. HARMS (1927) a décrit celle de *Macrotermes gilvus* à Buitenzorg (Java) ; mais l'information fournie par ce biologiste ne concerne que le creusement du copularium, l'apparition de larves (3 larves furent observées au 49^e jour suivant la fondation ; 18 œufs se trouvaient aussi dans le copularium). Cela tient en partie au fait que la plupart des fondations pratiquées par HARMS sont très anormales, car elles réunissent non un couple d'essaimants, mais jusqu'à 50 individus ! HARMS a signalé que les parois du copularium étaient faites de boulettes de terre agglomérées et lissées sur la face interne ; cet enduit se continuait insensiblement avec la terre avoisinante ; l'observateur en attribue la construction au couple lui-même. L'ébauche de meule a été vue, mais n'est ni figurée, ni décrite. Les larves du troisième stade, dont parle HARMS, sont, en réalité, de petits ouvriers, comme l'atteste leur comportement de terrassiers.

LÜSCHER (1951) a fourni quelques renseignements sur les premiers états d'une colonie de *Pseudacanthotermes spiniger*, mais plusieurs de ses observations ne se rapportent pas au comportement normal. L'élevage sur la sciure de bois prise dans un gel d'agar-agar ne permet pas aux Macrotermitinae d'accomplir leur comportement habituel. L'absence de bois cohérent et surtout d'argile a, sur la conduite de ces Termites, des conséquences apparemment très sérieuses. Elle rend la construction de l'habitable, des galeries couvertes, etc., pratiquement impossible. Il est à peine utile de rappeler que l'éthologiste, s'il désire aboutir à des résultats valables, doit placer les sujets en expériences dans des conditions aussi voisines que possible de celles de la nature.

Dans les élevages de LÜSCHER, aucune ébauche d'habitable n'a été faite et les ébauches de meules à champignons, d'ailleurs demeurées stériles, contenaient de la terre, ce qui paraît être anormal. L'absence d'amas de sciure de bois est probablement en rapport avec les conditions anormales de l'élevage.

CHRONOLOGIE DES PRINCIPAUX ÉVÉNEMENTS SE DÉROULANT AU COURS DES CENT CINQ
PREMIERS JOURS DE LA TERMITIÈRE.

| | |
|--|-----------------------------|
| Formation du couple | Jour 0. |
| Creusement du copularium | 10-12 heures. |
| Mutilation des antennes | ? |
| Premier coït | ? |
| Ponte du premier œuf | 15 jours (peut-être moins). |
| Éclosion de la première larve | 46 — |
| Apparition du premier petit soldat-blanc | 60 — |
| Premier petit ouvrier | 68 — |
| Premier petit soldat parfait | 76 — |
| Construction de galeries ascendantes | 88 — |
| Premier grand ouvrier | 95 — environ. |
| Construction de l'habitacle | 95 — |
| Premier amas de sciure de bois | 98 — |
| Première meule à champignons | 105 — (peut-être moins). |

Résumé.

D'après des élevages faits en Côte d'Ivoire, on décrit les premières étapes du développement pour les colonies de *B. natalensis*, en examinant particulièrement la construction du nid, la formation de la meule à champignon et des amas de sciure de bois.

Le couple imaginal fondateur creuse une cavité souterraine (copularium) où il élève, sans prendre aucune nourriture, la première couvée. Les premiers petits ouvriers creusent alors des galeries ascendantes par où ils vont attaquer le bois à la surface du sol, à l'abri de galeries couvertes. Les premiers grands ouvriers apparaissent peu après.

En une seule nuit, les ouvriers construisent, à l'intérieur du copularium, un habitacle régulier de forme ovoïde ; la première meule à champignons, d'emblée fertile, est édifiée à l'intérieur de cet habitacle ; la sciure de bois, réserve alimentaire, est amassée à l'extérieur.

Les homologues sont établies entre les structures et cavités du jeune nid et celles de la termitière adulte.

Summary.

Among the breedings carried out on the Ivory Coast, we could describe the first stages of development in colonies of *B. natalensis* especially, by observing their nest-building, the growth of the fungus bed and of the heaps of saw-dust.

The imaginal founder couple dig an underground cavity (copularium) in which they tend the first brood without taking any food themselves. Then, the first small workers dig ascending passage-ways through which they go in order to eat into the wood on the surface of the ground in the shelter of covered passage-ways. The first big workers come out soon after.

In one night, inside the copularium the workers construct an even egg-shaped dwelling-place; the first fungus bed, at once fertile, is erected inside this dwelling-place; the heaps of saw-dust used as food-reserves are laid outside.

Homologies are drawn between the structures and cavities of a young nest and those of an adult termitarium.

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**DIE BEDEUTUNG DES INNERSEKRETORISCHEN SYSTEMS
FÜR DIE AUSBILDUNG
EPIDERMALER KASTENMERKMALE BEI DER
HONIGBIENE (*APIS MELLIFICA* L.).**

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PROBLEMSTELLUNG

Königin und Arbeiterin der Honigbiene zeigen Unterschiede in der Körperform, der Körpergröße, der Ausbildung der Geschlechtsorgane und des Nervensystems, weiterhin im Stoffwechsel, in den Leistungen und am auffälligsten in der Größe von Epidermisbildungen, die als Kastenmerkmale bekannt sind (ZANDER u. BECKER, 1925). Die unterschiedliche Ausbildung derartiger epidermaler Kleinorgane: Haare des Körperstammes, Borsten der Sammelbeine, Härchen der Glossa, Wachsdrüsen, Duftdrüsen, Mandibeldrüsen und Futtersaftdrüsen konnte auf unterschiedliches Zellteilungsgeschehen in der Entwicklung zurückgeführt werden (LUKOSCHUS, 1954). In der gleichen Zeit zeigen die larvalen Oenocyten (deren Funktion noch umstritten ist) und die innersekretorischen Drüsen: die neurosekretorischen Zellen des Gehirns, die Corpora cardiaca, die Corpora allata und die Prothoraxdrüsen bei den Angehörigen der Kasten starke Unterschiede in Volumenentwicklung und Sekretionserscheinungen (LUKOSCHUS, 1952, 1954). Daß diese Drüsen, deren Bedeutung für Wachstum und Metamorphose bei vielen Insekten nachgewiesen wurde (Zusammenfassungen: PIEPHO, 1951; SCHARRER, 1952, 1953), bei der Biene die gleichen Funktionen ausüben, wurde durch Schnürungsversuche wahrscheinlich gemacht (L'HÉLIAS, 1951; SCHALLER, 1951, 1952; LUKOSCHUS, 1955). Es ist nun zu vermuten, daß das bei Königin und Arbeiterin stark unterschiedliche Hormonsystem bei der Entwicklung der Kleinorgane beteiligt ist, die während der Metamorphose erfolgt. Erste Hinweise auf eine Beeinflussung der Größenentwicklung von Borsten durch hormonelle Eingriffe gab KRUMINS (1952) bei *Galleria mellonella*. Jedoch sind die Literaturangaben über die Wirkung der inkretorischen Drüsen auf das Zellteilungsgeschehen nicht einheitlich.

Der Wundverschluß bei Hungertieren, deren Corpora allata weitgehend zurückgebildet sind, erfolgt durch Zellwanderungen, während bei

normal ernährten Tieren, die große und tätige Drüsen besitzen, lebhaft Zellteilungen erfolgen (WIGGLESWORTH, 1937). PFLUGFELDER (1939-1949) brachte ebenfalls die Zellteilungstätigkeit bei der Regeneration mit den Wirkstoffen der Corpora allata in Zusammenhang. BODENSTEIN (1953) fand eine Abhängigkeit der Anzahl der Zellteilungen von der Zeitdauer (in der das normale Hormonmilieu wirken konnte). Demgegenüber schließt BÖDEWADT (1951) aus seinen Zählungen an *Galleria* auf eine hemmende Funktion des Corpora allata-Wirkstoffes. Aus dem Versuchsausfall schließt er, „daß die Mitosenperiode als erster morphologischer Teilvorgang der Häutung der Epidermis... durch einen extraepidermalen, von der Leibeshöhle her direkt angreifenden stofflichen Faktor ausgelöst wird“. Es wird dabei vermutet, daß es sich hierbei um den Häutungswirkstoff selbst oder von ihm abhängige Stoffe handelt (Siehe auch PIEPHO, 1947). Ziel dieser Arbeit ist es nun, festzustellen, ob Entwicklungsvorgänge, die zur Ausbildung von Kleinorganen führen, durch hormonelle Eingriffe beeinflußt werden können. Damit sollen weitere hormonphysiologische Grundlagen zum Studium der Staatenbildung bei Insekten geschaffen werden.

Ich danke meinem verehrten Lehrer, Herrn Prof. Dr. H. PIEPHO, für die Anregung zu dieser Arbeit.

MATERIAL UND METHODE

Die Beobachtungen sind eine Fortführung der 1952, 1954 und 1955 dargestellten Untersuchungen. Bei den Transplantationsversuchen wurde die Bläschenmethode angewandt, die PIEPHO (1938) ausführlich beschrieben hat. Die Versuche wurden im Sommer 1952 im *Landesinstitut für Bienenforschung und bienenwirtschaftliche Betriebslehre in Celle* durchgeführt. Nur durch die großzügige Unterstützung von Herrn Dr. WOHLGEMUTH und die Mithilfe aller Angestellten und Schüler seines Institutes war es möglich, die ausreichende Anzahl von 2 600 Königinnen verschiedener Entwicklungsstadien, die zum größten Teile für die Implantationsexperimente benötigt wurden, zu erhalten. Fräulein Ursula Sievert danke ich für wertvolle Hilfe bei der Durchführung der Versuche.

I. — SCHNUERUNGSVERSUCHE

A. — Beobachtungen an Haaren und Borsten.

Wenn die humoralen Bedingungen für die Ausbildung von Kleinorganen untersucht werden sollen, ist es zweckmäßig, nicht den gesamten Komplex, sondern nacheinander Teilvorgänge zu beobachten. Nach KÖHLER (1932), STOßBERG (1938), HENKE (1947), SCHWENK (1947) können folgende Entwicklungsschritte getrennt voneinander beobachtet werden, obwohl sie sich zeitlich z. T. überschneiden :

1. die differentiellen Zellteilungen, in denen aus Stammzellen der Epidermis die Bildungszellen der wenigzelligen Kleinorgane entstehen; — 2. das Heranwachsen der Bildungszellen durch Endomitosen; — 3. die Formvorbildung der Cuticularstrukturen; — 4. die Bildung der Cuticula und die Pigmentierung.

Bei der Biene laufen die differentiellen Zellteilungen der Haare in der Vorpuppe ab. In der jungen Puppe wachsen die trichogenen Zellen endo-

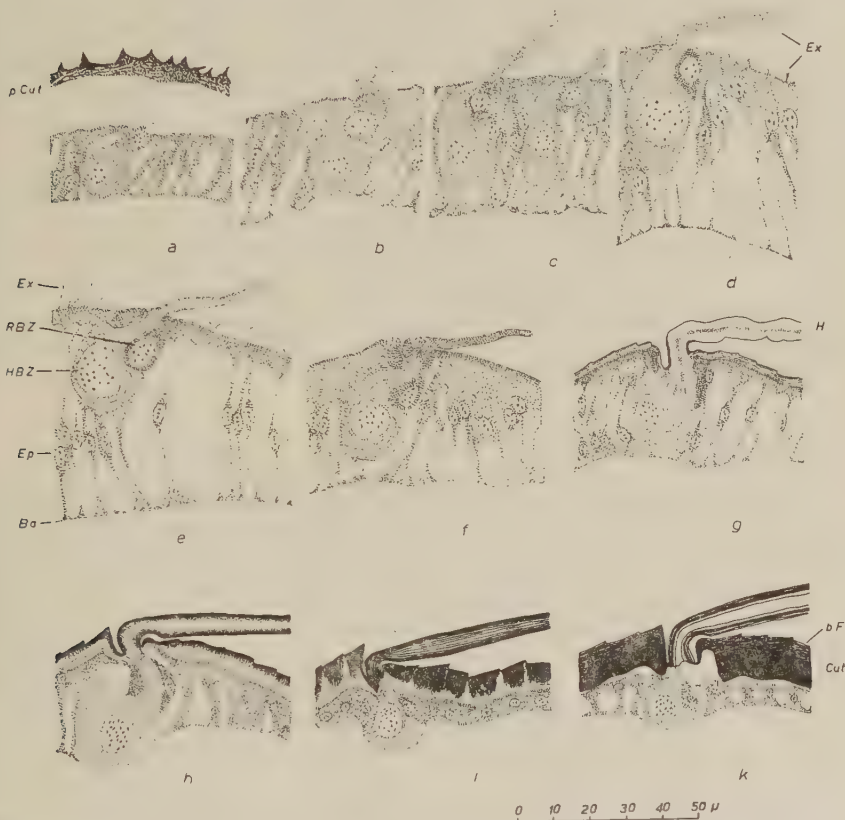


Abb. 1. — Imaginale Differenzierung des behaarten Integumentes während der Puppenzeit; a 10, b 15, c 25, d 37, e 55, f 67, g 87, h 100, i 115, k 135 Stunden nach der Puppenhäutung.

mitotisch heran (Abb. 1 a—d). Sie scheiden einen Plasmafortsatz aus (c—e), der sich verdichtet (f, g) und zu einem cuticularisierten Haar umwandelt (g, h), das sich in der späten Puppenzeit verfestigt (i) und anfärbt (k). Bei Schnürungsexperimenten wird der Blutkreislauf und damit die Verteilung stofflicher Faktoren im Körper unterbunden. Durch Variation des Schnürungszeitpunktes während der Entwicklungszeit und durch Anlegen der Ligatur an verschiedenen Körperstellen kann aus den Ergebnissen auf die Lage der Bildungszentren und aus der kritischen Periode auf den Zeitpunkt der Sekretion geschlossen werden.

a) *Cuticulabildung und Pigmentierung.*

Puppen, denen gleich nach der Puppenhäutung eine Ligatur hinter dem Kopf angelegt wird, entwickeln sich an Thorax und Abdomen normal weiter. An den Tergiten wächst aus den trichogenen Zellen der Plasmafortsatz aus, der sich cuticularisiert und anfärbt.

Wenn die Schnürung jedoch in der Wespentaille angelegt wird, entwickeln sich nur Kopf und Thorax normal weiter. Auch bei späten Schnürungsterminen (66—72 Stunden nach der Puppenhäutung) erfolgt keine weitere imaginale Differenzierung des Abdomens. Der zu diesem Zeitpunkt bereits ausgewachsene Plasmafortsatz der trichogenen Zelle (Stadium *f* der Abb. 1) versteift sich nicht und färbt sich nicht an.

Hieraus ist zu schließen, daß Faktoren des Thorax für den Vorgang der histologischen Differenzierung notwendig sind. Eine Beteiligung des Kopfes für diese Vorgänge ist vom Augenblick der Puppenhäutung an nicht mehr notwendig. Dieser Befund entspricht der Anschauung von SCHARRER (1952). Danach sind die Prothoraxdrüsen die Bildungsstätten eines „Wachstums- und Differenzierungshormons“, das für die imaginale Ausbildung des Integumentes von Bedeutung ist.

b) *Größenausbildung von Borsten.*

In der Normalentwicklung der jungen Puppe laufen in den trichogenen Zellen Endomitosen ab. Hochpolyploide Zellen bilden dann große, geringpolyploide Zellen kleinere Borsten. Falls die Größenausbildung der Borsten von Faktoren des Kopfes abhängig ist, können Schnürungen der jungen Puppe Aufschlüsse über den Zeitpunkt einer stofflichen Wirkung geben. Für einen Vergleich der Größenausbildung sind die Borsten der Sammlerferse besonders geeignet. Sie weisen nur sehr geringe Längenunterschiede auf und können ihrer gesetzmäßigen Anordnung wegen genau lokalisiert werden. Um exakte Längenmessungen an den von der Tarsusoberfläche abstehenden Borsten durchzuführen, wurden die zweite Borstenreihe von unten herausgeschnitten und Tarsusaußenseite und Hypodermis entfernt. Bei den schmalen in Euparal eingebetteten Streifen kommen die Borsten in ihrer ganzen Länge in die optische Ebene des Mikroskopes zu liegen. Gemessen wurden je 12 Borsten eines Tieres mit dem Okularmikrometer in Längenklassen von 8 μ . Die Ergebnisse von je 10 Tieren eines Schnürungsalters sind in der Abb. 3 dargestellt. Zum Vergleich wurden Messungen an Hungerformen durchgeführt, die vom Beginn des V. Larvenstadiums an ohne Futter waren.

Hieraus ist zu schließen : 1) Die Länge der Borsten ist abhängig von einem Faktor aus der Kopfregion. 2) Die kritische Periode für die Wirkung des Kopfes liegt bei etwa 15 Stunden nach der Puppenhäutung. Später geschnürte Tiere zeigen weitgehende Annäherung an die Kontrollen. Der mögliche Einwand einer unspezifischen Schädigung der Versuchstiere

scheidet deshalb aus. 3) Trichogene Zellen, in denen acht Endomitoseschritte abgelaufen sind, bilden Borsten von ca. $430\ \mu$ Länge. Gleiche Zellen, die nur vier Endomitosen durchmachten, ergeben Borsten von ca. $250\ \mu$ Länge. Dazwischenliegende Borstenlängen werden von Kernen mit intermediärer Polyploidiestufe gebildet. Durch eine Schnürung zum Zeit-



Abb. 2. — Entwicklung der trichogenen Zellen an den Borsten der Sammelferse bei der Königin (*a—e*) und bei der Arbeiterin (*a₁—i₁*) von der Puppenhäutung bis zum Beginn der Bildung der imaginalen Cuticula. Die Zahlen zwischen den Einzelabbildungen sind die mittleren Kernvergrößerungsfaktoren der aufeinander folgenden Endomitosestadien.

punkt der Puppenhäutung werden die Borsten derart verkleinert, daß sie Cuticularbildungen von trichogenen Zellen entsprechen, die in ungestörter Entwicklung zwei Endomitosen weniger durchlaufen haben. Bereits 5 Stunden später sind die Borsten nur noch so groß, wie sie Bildungszellen mit nur einem Teilungsschritt kleineren Kernen entsprechen. 4) Durch eine Beeinflussung zu einem früheren Zeitpunkt (Hunger vom Beginn des V. Larvenstadiums an) erfolgt eine stärkere Einwirkung auf das Größenwachstum der Borsten.

Durch Hunger bzw. mangelhafte Ernährung werden bei der Biene (MÜSSBICHLER, 1951) wie bei anderen Insekten (WIGGLESWORTH, 1936; KAISER, 1949; SCHWINCK, 1951) von den Inkretdrüsen des Kopfes besonders die Corpora allata beeinflusst.

Eine noch weiter gehende Störung der Größenentwicklung kann erzielt werden, wenn Spinnmaden geschnürt werden. Bei den dabei erhaltenen

Zwischenformen, deren Cuticula imaginal ausgebildet ist, sitzen an den Sammeltarsen sehr kleine (bis 100 μ lange) Borsten. Sie entsprechen Borsten der Normalentwicklung, deren Bildungszellen nur 1-2 Endomitosen durchliefen. Diese bereits durch SCHALLER (1951) beschriebene Beobachtung kann dann gedeutet werden, wenn angenommen wird, daß zu dieser Zeit die für die ersten 1-2 Endomitoseschritte erforderlichen stofflichen Faktoren von Organen des Kopfes ausgeschieden werden. Für weitere

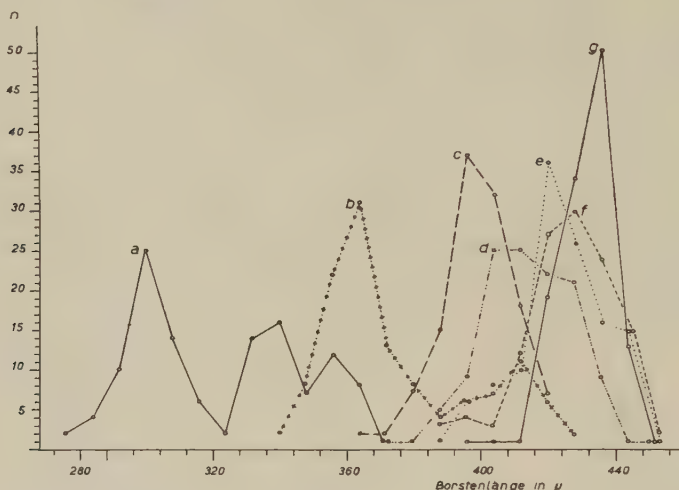


Abb. 3. — Längen der Borsten vom Sammeltarsus von kopfgeschnürten Arbeiterinnen und Hungerformen.

a Hungertiere.

b Kopfschnürung im Augenblick der Puppenhäutung.

c — 5 Stunden nach der Puppenhäutung.

d — 15 — — — —

e — 20 — — — —

f — 28 — — — —

trichogenen Zellen wie Abb. 1 c).

g Ungeschnürte Kontrolle.

Borsten von späten Schnürungsdaten und Thoraxschnürungen zeigen keine wesentlichen Abweichungen von den Kontrollen. Sie sind der Uebersichtlichkeit wegen nicht eingezeichnet.

Polyploidiesprünge sind durch die Ligatur die notwendigen Kopffaktoren ausgeschaltet, während die für die histologische Differenzierung erforderlichen Stoffe in Thorax vorhanden sind. Die kritischen Perioden für die Größenausbildung der Borsten liegen lange vor dem histologisch faßbaren Größenzustand der Kerne. Diese Erscheinungen können gedeutet werden, wenn angenommen wird, daß die Teilungen in den Chromosomen vorbereitet werden, lange bevor sie durchgeführt werden.

Ähnliche Verhältnisse fanden HENKE, VON FINCK und MA (1941) bei *Drosophila*. Die sensiblen Perioden für die Auslösung von Hitzemodifikationen der Borsten liegen lange vor dem Zeitpunkt der differentiellen Teilungen ihrer Bildungszellen. Mit wachsender Entfernung von der Mitosenperiode werden die erhaltenen Borsten immer kleiner, um schließlich bei Reizung in frühen Stadien überhaupt nicht ausgebildet zu werden. Auch Bestrahlungen an Mehlmottenvorpuppen vor dem Zeitpunkt der

differentiellen Zellteilungen zeigten Auswirkungen an verschiedenen großen Zellnestern. Die Zellteilungen, die zur Ausbildung dieser Nester führen, sind lange vor ihrem Ablauf in den Chromosomen der Stammzelle vorbereitet (POHLEY, 1953).

c) Die Entwicklung von Haaren.

In der Normalentwicklung erfolgen die differentiellen Teilungen, die zur Ausbildung der Haare führen, in der Mitosenperiode der Vorpuppe. Die durch eine schräge Spindelstellung besonders auffällige letzte Teilung, die Haar- und Ringbildungszelle entstehen läßt, findet bei großen Haaren früher als bei kleinen statt. Durch Kopfschnürungen zu verschiedenen Zeitpunkten kann geprüft werden, ob Faktoren des Kopfes für das differentielle Teilungsgeschehen von Bedeutung sind. Als Testorgan wurde die Behaarung des 9. Tergites ausgewählt. Dazu wurden 2 mm breite Streifen

| Haarform | glattes Haar | | | Stichelhaar | | Unterhaar | Fiederhaar | | Miss- bildung | n |
|----------------------|--------------|-------|-------|-------------|-------|-----------|------------|-------|------------------|------|
| Haarlänge in μ | - 50 | - 100 | - 200 | - 160 | - 260 | - 200 | - 260 | - 530 | | |
| Königin | 911 | 763 | - | 81 | 101 | | 35 | 63 | | 1954 |
| Zwischenform 1 | - | - | - | - | - | - | - | - | - | 0 |
| 2 | 16 | 1 | - | - | - | - | - | - | - | 17 |
| 3 | 220 | 54 | - | - | - | - | - | - | - | 274 |
| 4 | 258 | 104 | 5 | - | - | - | - | - | - | 367 |
| 5 | 214 | 191 | 121 | - | - | - | - | - | 3 | 529 |
| 6 | 201 | 175 | 149 | - | - | - | - | - | 16 | 541 |
| geschnürte Puppe | 10 | 68 | - | 696 | 286 | 123 | 73 | 104 | - | 1460 |
| Arbeiterin mellifica | 10 | 9 | - | 242 | 359 | 453 | 36 | 181 | - | 1290 |
| carnica | 2 | 10 | - | 290 | 324 | 773 | 5 | 168 | - | 1571 |

Abb. 4. — Haartypen und Haarlangenverteilung im mittleren Abschnitt der 9. Rückenschuppe bei Königin, Arbeiterin und Versuchstieren. Die Zwischenformen sind im gesamten Bereich des 9. Tergits vollständig imaginal inkrustiert und pigmentiert.

aus der Mittellinie der Rückenschuppe herausgeschnitten und bei den Zwischenformen direkt in *Euparal* eingebettet. Bei Arbeiterinnen, Königinnen und geschnürten Puppen war es wegen der großen Anzahl der gegliederten Haare erforderlich, die Tergitabschnitte vorsichtig quantitativ abzuschaben, die Haare auf dem Objektträger zu verteilen und in *Euparal* einzubetten. Die mit dem Okularmikrometer gemessenen Werte von typischen Tieren sind in der Abb. 4 zusammengestellt.

Bei den Versuchstieren, bei denen durch eine Schnürung die Hormonzentren des Kopfes und des Thorax getrennt sind, bei denen also im Hinterkörper der Hormonhaushalt gestört ist, treten folgende Erscheinungen an der Behaarung auf: 1) Bei einer Schnürung zu einem frühen Zeitpunkt der Spinnperiode bilden sich keine Haare aus (Zwischenform 1). 2) Zu einem etwas späteren Zeitpunkt bilden sich kleine Haare in geringer Anzahl (Zwischenformen 2, 3). Diese stehen an den Stellen der großen Haare der Normalausbildung (Abb. 5 a). 3) Zu einem noch späteren Zeit-

punkt sind die Haare z. T. größer. Auch ihre Anzahl ist größer. An den Stellen der kleinen Haare der Normalausbildung (Abb. 5 c) fehlen jedoch auch hier differenzierte Bildungen.

In der Abb. 5 sind gleiche Ausschnitte vom hinteren Teil der Rückenschuppe derartiger Zwischenformen und einer Kontrolle zusammengestellt. Die Verteilung der Haare bei den Zwischenformen läßt erkennen, daß es

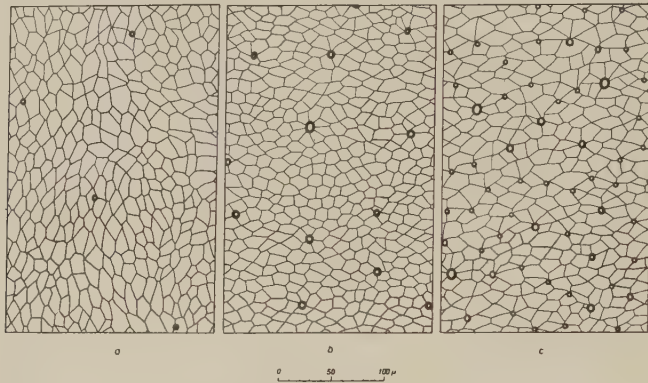


Abb. 5. — Aufsicht gleicher Teile der 9. Rückenschuppe a) einer Zwischenform vom Typ 3, b) einer Zwischenform vom Typ 6, c) einer Arbeiterin. Anordnung und Größe der Haare sind durch Halteringe dargestellt.

sich hierbei nicht um ein Gefälle handelt, das die Haare nur am Rande des Tergites entstehen läßt. Zwischen den Halteringen liegen bei a) und b) viele der durch ihre Cuticularrandbildung kenntlichen Epidermiszellen (siehe den Schnitt der Abb. 1 i, k), bei der Kontrolle c) jedoch stets nur wenige.

Die Aufsicht auf eine Puppencuticula läßt keine Grenzdifferenzierungen zwischen den Cuticularbildungen der einzelnen Hypodermiszellen erkennen. Die für die Puppencuticula charakteristischen kleinen Erhebungen sind im Längsschnitt in der Abb. 1 a dargestellt (vergl. mit Abb. 1 k).

Die Schnürungen erfolgten zeitlich vor den differentiellen Zellteilungen. Hieraus kann gefolgert werden: 1. Die differentiellen Teilungen, welche die trichogenen Zellen entstehen lassen, sind abhängig von Faktoren des Kopfes. 2. Die kritische Periode für die Bildungszellen der großen Haare liegt früh, die für kleinere Haare liegt später.

B. — Beobachtungen an Drüsen.

Entwicklung und Größenwachstum der Duftdrüsen.

Die Duftdrüsen der Arbeiterin entwickeln sich durch differentielle Teilungen aus Stammzellen der Epidermis. Diese Zellteilungen erfolgen während der Mitosenperiode der jungen Puppe. In der Folgezeit wachsen

die Kerne der Drüsenzellen stark heran, die einzelnen Drüsenelemente Drüsenzelle, Schaltzelle und Kanalzelle (F) differenzieren sich und bilden das cuticularisierte Ausführkanälchen. Dieser Differenzierungsvorgang ist bereits bei Beginn der Inkrustierung und Pigmentierung der imaginalen Cuticula nicht zu verkennen. Bei den geschnürten Spinnmaden ist bei den weitgehend imaginal abgewandelten Zwischenformen die Cuticula in völlig imaginaler Form ausgebildet, inkrustiert und pigmentiert. Duftdrüsen sind jedoch nicht zu finden. Bei den geschnürten Puppen sind sie in normaler Anzahl, nicht aber in der dem Entwicklungsstadium entsprechenden Größe vorhanden. Hieraus kann geschlossen werden, daß Faktoren aus der Kopfreion in der späten Vorpuppenzeit für die Ausbildung der Duftdrüsen (d. h. für die differentiellen Zellteilungen) und in der jungen Puppe für das Größenwachstum der Drüsenzellen notwendig sind.

Größenwachstum der Wachsdrüsenzellen.

Bei den früh geschnürten Puppen, deren Cuticula normal imaginal ausgebildet ist, fehlen differenzierte vergrößerte Wachsdrüsenzellen. Bei später geschnürten Tieren sind die auffällig vergrößerten Zellen und Zellkerne der Normalausbildung vorhanden.

Das Heranwachsen der Wachsdrüsenzellen unter Kernvergrößerung ist also von Faktoren des Kopfes abhängig.

GEMEINSAME GRUNDZUEGE IN DER BEEINFLUSSUNG EPIDERMALER KASTENMERKMALE

Die untersuchten Merkmale : Behaarung des Abdomens, Behorstung des Sammeltarsus, Duftdrüse und Wachsdrüse zeigen übereinstimmend bei der Arbeiterin mehr Teilungsschritte als bei der Königin. Diese als Mitosen und Endomitose ablaufenden Chromosomenvermehrungen sind nach den Schnürungsversuchen von Faktoren des Kopfes abhängig.

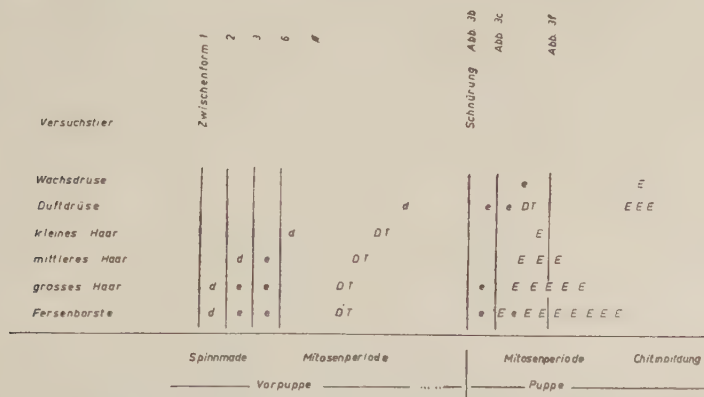


Abb. 6.

In dem Schema (Abb. 6) ist die zeitliche Aufeinanderfolge der histologisch gefundenen differentiellen Teilungen (DT), des Kernwachstums (E = Endomitosen) und der experimentell erschlossenen kritischen Perioden für Organentwicklung (*d*) und Größenwachstum (*e*) dargestellt worden. Zur Ausbildung kommen nur die Entwicklungsvorgänge, deren kritische Periode der Beeinflußbarkeit durch Kopfschnürungen zeitlich vor dem durch einen senkrechten Trennungsstrich dargestellten Schnürungstermin liegt.

Frühe Schnürungen, das bedeutet geringe Mengen eines Wirkstoffes, führen zu kleiner Ausbildung, späte Schnürungen, d. h. große Mengen, zur normalen Ausbildung, zu den großen Formen der Arbeiterin.

Von den inkretorischen Organen des Kopfes, die hierbei während der

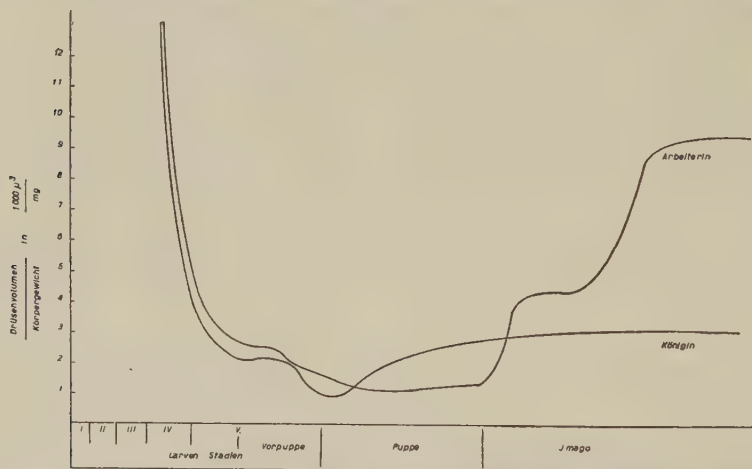


Abb. 7. — Berechnung des Volumens der Corpora allata auf das Körpergewicht während der Entwicklung von Königin und Arbeiterin.

gefundenen kritischen Perioden eine Rolle spielen könnten, zeigen bei den Angehörigen der Bienenkasten nur die Corpora allata Verhältnisse, die dieser Anschauung entsprechen. Wenn man das Drüsenvolumen auf das Körpergewicht bezieht, sind die Corpora allata der Königin in diesem Zeitraum kleiner als die der Arbeiterin. Andererseits fand ich bei meinen histologischen Untersuchungen dieser Drüsen, daß bei der Königin die stärkeren Sekretionserscheinungen festzustellen sind.

II. — IMPLANTATIONSVERSUCHE

Implantationen von Corpora allata.

Aus den Ergebnissen der Schnürungsversuche ist zu vermuten, daß durch die verhinderte Verteilung von Faktoren aus der Kopffregion bei der Arbeiterin Verhältnisse geschaffen werden, die denen der Königin ent-

sprechen. In Exstirpations- und Implantationsversuchen sollte überprüft werden, ob die nach Abb. 7 zu vermutende Bedeutung der Corpora allata sich erweisen läßt.

Die umfangreichen Versuche wurden beeinträchtigt durch die hohe Sterblichkeit der Versuchstiere. Diese ist zurückzuführen auf :

1. das Fehlender Gerinnungsfähigkeit des Blutes,
2. die Bedingungen in dem für steriles Arbeiten nicht eingerichteten Bieneninstitut. Kleine Reste nicht entfernter Hämolymphe oder Exuvialflüssigkeit führten oftmals zum Verpilzen der Tiere,
3. auf Schädigungen, welche die Königinlarven während des Transportes von den teilweise entfernten Außenständen erlitten hatten, die aber bei der Durchführung der Versuche noch nicht zu erkennen waren.

Es ist mir nicht gelungen, die seitlich des Oesophagus liegenden Corpora allata zu entfernen.

Das unterschiedliche Drüsenvolumen bei den Kasten sollte deshalb untersucht werden durch Implantation von Arbeiterin-Corpora allata in die Königin; kasteneigenen Drüsen in die Königin; die unterschiedliche Stärke der Sekretionserscheinungen durch Königin-Corpora allata in der Arbeiterin; Summierung von Arbeiterin-Drüsen in der Arbeiterin. Zur Kontrolle wurden Teile des Fettkörpers implantiert. Bei den vier verschiedenen Serien konnte keine bemerkenswerte Abweichung in der Ausbildung der Kleinorgane festgestellt werden.

Implantationen von Prothoraxdrüsen.

Es könnte nun sein, daß nicht das relative Volumen einer Drüse, der Corpora allata, für die Ausbildung ausschlaggebend ist, sondern das Verhältnis der beiden für die Metamorphose bedeutsamen Drüsen. Dieses als Hormonmilieu bezeichnete Zusammenwirken von Corpora allata (*Jugendhormon*) und Prothoraxdrüse (*Wachstums- und Differenzierungshormon*) ändert sich bei jedem daraufhin untersuchten Objekt im Laufe der Entwicklung. Während der Vorpuppen- und Puppenzeit wird es weitgehend zu Gunsten der Prothoraxdrüsen verschoben (KAISER, 1949). Auch zwischen den Kasten der Honigbiene bestehen Unterschiede, die auffälliger sind als die Volumenunterschiede der Corpora allata allein. Implantationen von Königin-Thoraxtracheen mit anhängenden Prothoraxdrüsen während der histologisch festgestellten Sekretionsperiode in die frischgehäutete Arbeiterin-Puppe ergaben starke Beeinflussungen der Kastenmerkmale. In der Abb. 8 sollen Teile der Futtersaftdrüse eines kurz vor der Imaginalhäutung stehenden Versuchstieres mit den Drüsen gleicher und jüngerer Stadien der Normalausbildung verglichen werden. Es zeigt sich dabei, daß nur sehr wenige der Einzeldrüsen vorhanden sind, welche in der Normalausbildung die Pseudoacini der Futtersaftdrüse entstehen lassen. Eine cuticularisierte Ausbildung der Sammelkanals ist nur in Andeutung an den Stellen vorhanden, an denen die einzelnen Drüsenkanälchen münden.

Die den Sammelkanal bildenden Epidermiszellen, die in der Normalausbildung nach der Cuticulaabscheidung weitgehend zurückgebildet werden, sind bei den Versuchstieren so großvolumig wie Zellen aus Imaginalscheiben.

Es kann hieraus geschlossen werden :

1. Nur bei einer geringen Anzahl der zum Implantationszeitpunkt

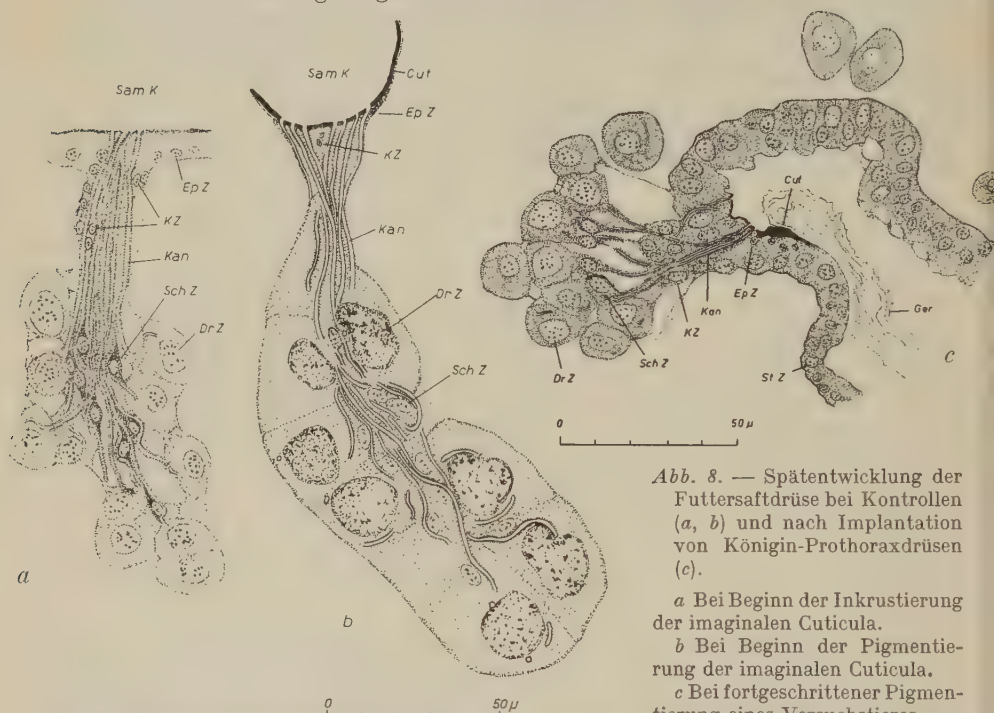


Abb. 8. — Spätentwicklung der Futtersaftdrüse bei Kontrollen (a, b) und nach Implantation von Königin-Prothoraxdrüsen (c).

a Bei Beginn der Inkrustierung der imaginalen Cuticula.

b Bei Beginn der Pigmentierung der imaginalen Cuticula.

c Bei fortgeschrittener Pigmentierung eines Versuchstieres.

Cut, Cuticulaauskleidung des Sammelkanals ; Dr Z, Drüsenzelle ; Ep Z, Epithelzelle ; Ger, Gerinnsel im Sammelkanal ; Kan, Ausführkanälchen ; KZ, Kanalzelle ; Sam K, Lumen des Sammelkanals ; Sch Z, Schaltzelle ; St Z, undifferenzierte Stammzellen.

vorhandenen Drüsenstammzellen der Drüsenanlage sind die differentiellen Zellteilungen abgelaufen.

2. Nach der histologischen Differenzierung der Einzelelemente hat ein geringes Größenwachstum der Drüsenzellen stattgefunden.

3. Die Stammzellen, die sich nicht geteilt haben, scheinen nicht die Fähigkeit zu besitzen, eine Cuticula zu bilden.

III. — TRANSPLANTATIONEN DER INNENSEITE DES SAMMELTARSUS

Wenn Veränderungen des agierenden Systems für das Größenwachstum von Merkmalen von Bedeutung sind, dann sollten Versuche mit dem reagierenden Gewebe die gleichen Erscheinungen zeigen. Hierzu wurde nach der

Bläschenmethode (PIEPHO, 1938) die Anlage der Sammelbürste in das Abdomen implantiert. Königintarsus in der Arbeiterin und Arbeiterintarsus in der Königin müßten Abweichungen in der Längenausbildung der Borsten zeigen. Obwohl fast 1 300 Königinnen für diese Versuche verbraucht wurden, konnten nur 82 Bläschen erhalten werden. Die Borsten zeigen Unterschiede zwischen homoplastischen und heteroplastischen Transplantationen und bestätigen damit die Ergebnisse der Schnürungsversuche und der Prothoraxdrüsenimplantationen.

Da es jedoch nach WIEDBRAUCK (1953) fraglich erscheint, ob bei Bläschenversuchen die Länge von Cuticularbildungen überhaupt betrachtet werden darf, soll von der Darstellung der umfangreichen Versuche abgesehen werden.

BEURTEILUNG DER ERGEBNISSE

In den geschilderten Versuchen ist es gelungen, durch Schnürungen zu verschiedenen Zeitpunkten, Drüsenimplantationen sowie Organtransplantationen (deren Beweiskraft jedoch fragwürdig ist), Entwicklungsvorgänge, die zur Ausbildung von Kastenmerkmalen führen, zu beeinflussen. Nachdem durch Beobachtung des Entwicklungsverlaufes das zeitliche Nacheinander von Futterwechsel, Größenausbildung und Sekretion der innersekretorischen Drüsen und Ausbildung der Kastenmerkmale festgestellt wurde, können die Versuche als experimentelle Bestätigung der vermuteten Abhängigkeit der Merkmalsausbildung vom Hormonsystem angesehen werden. Es zeigte sich dabei, daß Faktoren des Kopfes für die Zellteilungsvorgänge, die zur Entwicklung der Kleinorgane aus Stammzellen der Epidermis sowie zum Größenwachstum der Bildungszellen führen, von Bedeutung sind. Wirkstoffe der Prothoraxdrüse beenden diese Vorgänge. Sie bewirken die histologische Differenzierung der Zellen und die Ausbildung der Cuticula. Bei der Honigbiene scheint das mengenmäßige und zeitliche Zusammenwirken der beiden in Kopf und Thorax lokalisierten Hormonzentren für die Ausbildung der Kastenmerkmale von Bedeutung zu sein. Von den Merkmalen, die ZANDER und BECKER (1925) anführen, wurden in diesem Zusammenhange nur die Organe, die als Cuticularbildungen (Haare und Borsten) und Drüsen der Epidermis (Wachsdüse, Duftdrüse und Futtersaftdrüse) entstehen, beobachtet. Die Geschlechtsorgane, deren Abhängigkeit von Hormonen während des Imaginalstadiums von ALTMANN (1952) und MÜSSBICHLER (1952) untersucht wurden, sollen in ihren Erscheinungen während der Metamorphose gesondert dargestellt werden.

Darüber hinaus ist die Bedeutung des Hormonsystems für weitere Kasteneigentümlichkeiten wahrscheinlich. Die hormonell gesteuerte Stoffwechselintensität wird meßbar in der Entwicklungsgeschwindigkeit und führt zur Wärmeproduktion. Diese wiederum steht in Verbindung mit typischen Instinkthandlungen (LUKOSCHUS, 1955 a, b). Weitere Korre-

lationen zu Besonderheiten des Zwischenstoffwechsels machen wahrscheinlich, daß das Hormonsystem mit zentraler Wirkung zwischen Futterwechsel und Kastenausbildung eingeschaltet ist.

Für den ersten Teil der Kette : Futter - Drüsen - Kastenausbildung ist bislang nur für die Corpora allata der Abhängigkeitsnachweis geführt (MÜßBICHLER, 1952). Ihre Ergebnisse an der erwachsenen Biene stehen in Uebereinstimmung mit den Beobachtungen an Larven und Imagines verschiedener Insekten. Für die übrigen Hormondrüsen sind derartige Abhängigkeiten noch nicht bekannt. Es ist wahrscheinlich, daß „Ektohormone“ der Arbeiterin (BETHE, 1932) eine Rolle dabei spielen. Diese Verhältnisse sollen gesondert untersucht werden.

Zusammenfassung.

Durch Schnürungsversuche, Drüsenimplantationen und Organtransplantationen können bei Metamorphosestadien der Honigbiene Entstehung und Größenausbildung von Haaren, Borsten und Drüsen beeinflußt werden.

Faktoren des Kopfes sind für Entstehung und Größenausbildung, Hormone der Prothoraxdrüse für die histologische Differenzierung der Kleinorgane von Bedeutung.

Das innersekretorische System ist zwischen die Determination durch den Futterwechsel und die Ausbildung von Kastenmerkmalen eingeschaltet.

Summary.

By stringing experiments, implantation of glands, and transplantation of „Anlagen“ within the praepupal and nymphal stages of the honeybee the formation and the enlargement of hairs, bristles, and epidermal glands is influenced.

There are factors of the head responsible for the formation and the enlargement of the few-cell-organs, hormones of the prothoracic glands for their differentiation.

The endocrine system is acting between the caste determination by change of larval food and the development of caste differentiation.

Résumé.

La formation et la croissance des poils et des glandes épidermiques sont influencées par les expériences de ligature, d'implantation de glandes et de transplantation d'organes sur les prénymphes et les nymphes de l'Abeille.

La naissance et l'accroissement des petits organes sont sous la dépendance de facteurs localisés dans la tête, alors que leur différenciation histologique est conditionnée par des hormones prothoraciques.

Le système endocrine intervient entre la détermination de la caste sous l'influence de la nourriture larvaire et le développement des caractères différentiels de la caste.

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ADDITIONAL TECHNIQUES FOR STUDYING THE BEHAVIOR OF WILD BEES (1)

by

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The following notes are intended primarily as a supplement to a recent paper (LINSLEY, MacSWAIN and SMITH, 1952) on methods of studying the life histories of bees. Those authors present a useful checklist which serves to remind the student of bee ethology of most of the items that he should observe and record. Their discussion and listing are not oriented toward the study of the social *Halictidæ*, which live in colonies of small size in burrows, usually in the soil. Because of the complex relationships that exist among the individuals of such a colony, more detailed and painstaking observations and additional techniques are needed if the life history is to be understood. Our study of the literature on halictid and other bees shows many instances where authors could easily have provided critical information had they thought to do so or had appropriate techniques occurred to them. It is hoped that the following descriptions of techniques will encourage others to undertake the study of bee behavior and to provide needed data on such matters as female caste differentiation, longevity of queens and workers, and division of labor and integration among individuals of a colony. Many of these same techniques are also applicable to studies of solitary bees and wasps.

RELATIVE AGE OF BEES

It is often important to know as much as possible about the relative ages of bees. Mandibular wear of females is sometimes a guide to age, and has proved especially useful in studies of *Lasioglossum* (*Chloralictus*) *stultum* (Cresson). It is of much less use among certain bees (e. g. *Augochlorella*) which construct only small nests. It is usually most convenient to describe the mandibular wear by assigning each individual to one or another class. The classes should be determined separately for each species after a study of mandibles of a good series of dead specimens. In *L. stultum*, for example, mandibles of each individual are classified as (1) unworn, (2) slightly worn, (3) well worn, (4) much worn, or (5) very

(1) Contribution number 890 from the Department of Entomology, University of Kansas, Lawrence, Kansas, U. S. A. This study was conducted with the aid of a grant from the National Science Foundation.

much worn. A sketch of a median individual in each class serves as a guide for placing all others.

In most species of bees the wing margins become tattered with age. As with the mandibles, the degree of wear may be classified to provide an index of relative age. Also, the pubescence of the body may fade in color or even wear off as the bee grows older. All these characteristics were used in elucidating the overlapping generations of *Megachile brevis* Cresson, a solitary bee (MICHENER, 1953). The number of enlarged oocytes in the ovaries may also be used to judge age (BOHART and CROSS, in press), although there is some danger of confusing young with senile individuals.

Bees distinctively marked when young, released, and later recaptured, may be used to relate relative age, determined as suggested above, to actual age.

MARKING OF INDIVIDUALS

Various methods of marking individual bees are discussed by LINSLEY, MACSWAIN and SMITH (1952). Marking of all females in a small colony such as that of a *Halictus* or *Lasioglossum*, so that each can be followed as an individual, is extremely important. We have used primarily bright, quick drying paints having acetone or amyl acetate as solvents and continue to have some trouble with spots of such paint wearing off. The paint is applied with a fine brush while holding the bee firmly between thumb and finger. A marking system employing the same number of colored spots on each bee is desirable since if a spot wears off, its loss is obvious; in a system using varying numbers of spots, the loss of a spot would seem to convert one bee into another, resulting in false information.

The system of marking can be devised in accordance with the population size being investigated. We have found that the number of bees that can be marked with a two-spot abdominal marking system can be doubled by using pairs of transverse or of longitudinal marks. We have been able to use two or three-spot marking systems on *Lasioglossum stultum*, a bee only 4.5 to 5.0 mm long, the third spot being placed on the dorsum of the thorax. Larger bees are easier to mark except that they often sting more easily while held in the fingers. Great care must be taken not to allow the paint to get on the wing bases, eyes, or antennae. Furthermore, the paint must be allowed to dry thoroughly before the bee is released so that the paint will neither stick the wings down or get covered with dirt. Sometimes bees hampered by improperly placed paint can be scraped clean or wiped clean with solvent. Occasionally it is convenient to place bees inside a cardboard box where the paint can dry completely while the bee is quiet in the dark.

To mark bees in colonies of *Halictus* or *Lasioglossum*, we often suck them from the nest with an aspirator (see PETERSON, 1953), putting a little cotton in the aspirator bottle so that the bees will not be injured by

striking the hard glass or plastic. The cotton also serves to slow the movements of bees so that they may be taken more easily from the bottle with the fingers.

In halictid colonies some bees often stay in the nest most of the time and may not become conditioned to the landmarks in the environment. Perhaps for this reason many bees sucked from nests formerly disappeared after being marked and released. Losses were much reduced by reintroducing each marked bee into its nest. This is done by holding against the nest opening a short glass tube having an inside diameter about that of the entrance. The bee is then put into the top of the tube, head down. It crawls down the tube and thence into its nest. If it does not crawl readily it may be prodded with a straw.

In larger colonies of *Lasioglossum stultum* sentinels at the entrance, when disturbed by a straw or grass blade, bite at it, then, if the disturbance continues, turn and block the entrance with the dorsal posterior part of the abdomen. The bee is usually very firmly braced by its legs in this position, and the abdomen can readily be marked. This sentinel behavior makes subsequent records of sentinel activity convenient for, to see the markings, one need only cause the sentinel to block the hole with its abdomen.

As mentioned above, paints tend to wear off. A more permanent marking system has therefore been used for determining the longevity of queens, which frequently survive for as long as a year. They do not often leave the nests during the summer and hence cannot be remarked when their spots begin to disappear. Instead of marking the body with paint, the wings are stained with a saturated alcohol or acetone solution of methyl or ethyl eosin. This material is not water soluble and remains permanently on the wings. Bees treated in this manner may be recognized on sight by their red wings or by placing them on filter paper moistened with alcohol.

OBSERVATIONS OF ARRIVALS AND DEPARTURES

When bees are coming and going frequently from a nest, the observer ordinarily has no trouble obtaining the necessary data. A leaf or some fine straws placed above the entrance may be useful to slow fast moving marked bees so that their color spots can be accurately observed.

Often bees come and go so rarely that observation becomes tedious and the observer's time can well be devoted to more than one nest. It was found that a useful way to enable an observer to watch as many as 30 or 40 nests at a time, if they are reasonably close together, is to place small cones of wire screen over the entrances of the nests. Then as a bee leaves her nest she is trapped in the cone. The observer sees the bee crawling about inside the cone, records the departure of the particular bee, and releases it. The bees seem little disturbed by this and are rarely delayed for more than a minute or two. We found the method effective

in a study of *Nomia triangulifera* Vachal, *Halictus parallelus* Say and *Andrena erythronii* Robertson. Because of the difficulty which members of the latter species seem to experience in finding their nests under the best of circumstances, we usually removed the cone completely when an *Andrena* left. Cones were also tried with *Augochlorella*. However, because these bees seemed so "timid", we feared that their behavior would be unduly influenced by the cones.

The cones are simple to make by stapling the screening together and convenient to carry because they can be stacked.

DESTRUCTION OF EXCESS BEES

One of the complicating features of studying colonies or aggregations of bees is the number of individuals that may be working close together. Destruction of some may be the most satisfactory way of solving certain problems. Thus NOLL (1931), in transferring the cell clusters of *Lasioglossum malachurum* (Kirby), left behind or destroyed the queens. He thus obtained data on the behavior of queenless colonies and on the sex of the offspring known to arise from unmated workers.

MALYSHEV (1926) found nests of *Andrena vaga* Panzer (= *ovina* Klug) so close together in aggregations that they could not easily be differentiated when dug. He therefore killed females whose nests were close to those selected for observation and subsequent excavation. Similar techniques may at times be helpful with halictids.

EXCAVATION OF ADJACENT NESTS

The use of differently colored plaster of Paris for pouring into adjacent nests has value in distinguishing the nests as one digs them, especially when they are much branched and entangled with one another, as is often the case with *Lasioglossum* (*Chloralictus*) *versatum* (Robertson). Dried tempera pigments worked very well for this purpose. It is advisable to mix the pigment and water first and then add the plaster so that the color can be thoroughly mixed before the plaster starts to set. The plaster should be colored intensely so that if there is any seepage of the colored water between tunnels the nests can still be told apart.

POPULATION ESTIMATES

LINSLEY, MACSWAIN and SMITH (1952) discuss methods of determining population fluctuations. Actual populations, active at a given time in local areas of aggregation (such as a group of bee nests where dispersal of marked bees from the nesting area probably scarcely occurs), may be estimated by means of the Lincoln Index as follows: First, mark a number of bees in an aggregation. Then when the marked bees have resumed

normal behavior, make a census of the number of marked and of unmarked bees seen in a certain time period.

It may be assumed that the ratio of total marked (M^t) to unmarked bees actually in the area is equal to the ratio of marked (M^c) to unmarked (U^c) bees counted in the census. Therefore the following formula should give the total population (P) in such an aggregation where dispersal can be ignored.

$$\frac{M^t}{P} = \frac{M^c}{M^c + U^c} \quad \text{or} \quad P = \frac{M^t (M^c + U^c)}{M^c}$$

This method was used to estimate the population in a temporary aggregation of *Megachile brevis* by MICHENER (1953). It has also been used for other organisms, for example hares (GREEN and EVANS, 1940). BAILEY (1952) describes various modifications of this method. It should also be mentioned that where complications of dispersal and mortality are involved, methods of estimating actual populations have been devised, using marked individuals as a basis [see, for example, JACKSON (1940), DOBZHANSKY and WRIGHT (1947), and BURLA *et al.* (1950)].

CASTE DIFFERENCES

In the halictids the overwintering queens are usually reported to be larger than the workers. The extent to which this is true should be determined. We assume that a measurement of forewing length or of some portion thereof provides a reasonably satisfactory index of size. Such a measurement has recently been used with bumblebees (MICHENER and LA BERGE, 1954).

In determining which females are queens and which are workers, it is usually necessary to dissect them. In many species young females produced in the fall mate and then overwinter. Therefore, the presence of sperm cells in the spermatheca in spring or summer indicates an overwintering individual until the time when males appear. However, the existence of sperm cells in the spermatheca after males appear is not necessarily evidence that a bee is a queen since occasional inseminated females, almost certainly workers, have been found in *Lasioglossum stultum*. So far as our observations go, overwintering individuals are all queens, although until spring their ovaries are slender. In spring and summer, all three ovarioles of each ovary in queens become more or less equally enlarged. An occasional female, at least in *Lasioglossum stultum*, may have only one ovariole in one or both ovaries swollen. Such bees are workers but probably lay an occasional egg. NOLL (1931) believed that unfertilized workers of *L. malachurum* lay most of the male-producing eggs.

Worn mandibles combined with slender ovaries probably indicate a worker, that is, an old bee whose ovaries have not enlarged. Females having unworn mandibles and slender ovaries may be of either caste

although it is possible in the species that have clearly separated generations (e. g. *L. malachurum*) to judge by season alone the caste to which young females belong.

We have observed differential consumption of pollen by queens and workers and therefore record the presence or absence of pollen in the gut of each bee dissected.

To learn as much as possible of the habits of these bees and of caste differences, it is desirable to record for each individual dissected, (1) the size of the ovaries, (2) the number of enlarged ovarioles, (3) the number and size of the large oocytes, (4) the presence or absence of sperm cells in the spermatheca, (5) the approximate amount and position of pollen in the gut, (6) the length of the wing, (7) the amount of wing wear, and (8) the amount of mandibular wear.

To obtain the maximum information without destroying too many nests, it is important to collect series of specimens, preferably at weekly intervals, at some distance from known nests. These may then be dissected and the information indicated in the preceeding paragraph recorded. Data from series of such specimens from all seasons of the year should give an excellent idea of many features of the biology of a species even if few nests can be located for study.

Bees are dissected most easily after fixation for a few days in Kahle's (DIETRICH's) solution (LEE, 1937); they are killed in it and kept there until dissected. For the beginner fresh material is useful because the minute spermatheca is yellowish and therefore easily recognizable; it loses its distinctive color in Kahle's solution. Spermathecae dissected from living specimens should be placed on a slide in a drop of physiological saline solution. If such a spermatheca containing sperm cells is crushed the very long sperm cells can easily be seen and are usually motile. Spermathecae from fixed specimens are placed on a slide in a drop of water or fixative. When pressed under a coverslip the spherical mass of sperm cells is forced out of the spermatheca and, being quite elastic, returns to its spherical form unless very severely crushed. These methods become quite easy after a little experience so that sectioning is quite unnecessary. In fact, in fixed specimens it is usually possible to tell whether sperm cells are present in large numbers or are absent because under the binocular dissecting microscope the spermatheca is opaque when full of sperms, transparent when not full. Spermathecae with only a few sperms have not been found in spite of some search, although specimens with the spermatheca half full are known.

DIVISION OF LABOR

Among colonial halictid bees, any light that can be shed on division of labor is of special interest because of the primitive and often incipient nature of their social organization. Studies of behavior of marked

individuals are of primary importance in this connection. A matter of unusual interest has been to determine, for every species, whether each bee provisions its own cells or whether bees cooperate in this matter. One approach to this problem is to capture, during the few hours before digging a nest, all returning pollen carriers. A comparison of the number of cells being actively provisioned with the number of pollen collectors gives some information on the number of bees carrying pollen per cell being provisioned (APTEL, 1931).

A more positive method of getting information on this subject consists of mixing recognizable particles with the pollen being carried into a nest which is soon to be dug. Powdered charcoal, graphite, metallic powders of various kinds, as well as powdered pigments have been used for this purpose. We use, when possible, nests in which each pollen collector has been individually marked with colored paints for visual recognition. With an aspirator we catch each pollen carrier as she returns to the nest. Taking care not to dislodge the pollen load, we dust the bee with powder by means of a fine brush, a different colored powder being used for each bee, the same color for any particular bee each time she returns. The bee is then released and after a considerable time, at least with *Lasioglossum stultum*, she returns in an apparently normal manner carrying both pollen and powder and enters the nest. When the nest is dug the colored powders are found intermixed with pollen in the pollen balls. A binocular microscope is usually necessary to detect the colored particles.

To avoid disturbance of the bees another method was devised. A little powder is placed in a small glass tube and blown at the pollen laden bee just as she raises her abdomen to enter the nest. If properly done, powder is lodged on the bee without her being blown away. A danger exists in that some powder may fall into the nest and affect the results.

Observations of bees in nests.

The activities of bees inside nests in the soil are difficult to determine except by indirect methods. Such a method that has proved useful with *Andrena erythronii* and sometimes with halictids is to brush or blow the tumulus away at each visit to the nest. New soil pushed up will then be obvious and probably indicates continued digging by the bee.

A direct method that has proved valuable is to dig down beside a nest and either install glass windows made of microscope slides or coverslips in the burrow, or replace the upper part of the burrow by a glass tube. The details of the activities in the upper part of the nest may then be observed, as bees (preferably marked for individual recognition) go up and down. The excavation may be darkened by a covering to reduce possible abnormalities in behavior due to light in the nest, and may be made large enough so that the observer can lie in it and make his observations by means of a flashlight.

Our attempts to get halictine bees to make use of whole glass nests or glass cells have been essentially unsuccessful, although one bee (*Lasioglossum stultum*) did remain in a glass nest for a month. It came and went but never stored pollen or even worked in a cell. It should be pointed out, however, that NOLL (1931) was successful in moving nests containing immature stages of *Lasioglossum malachurum*. He placed the cell cluster in a hole dug to the appropriate depth in the soil, covered it with an inverted flower pot, and filled the space around the pot with soil. The bees, when they emerged, ordinarily did not use the small hole at the top of the flower pot but burrowed under the edge of the pot and then to the surface through the soil.

Summary.

This supplement to a paper by LINSLEY *et al.* (1952) describes techniques for the study of social *Halictidæ* as well as other bees. Methods used to judge relative ages of bees include study of mandibular wear and wing wear. Marking of individuals with quick drying paints is described. Marked bees may be returned to their nest through a glass tube. Paints often wear off; more permanent marking may be achieved by staining wings with an alcohol or acetone solution of methyl or ethyl eosin. Methods are described for delaying bees as they enter or leave their nest, so that color markings can be more easily seen. Small wire screen cones placed over nest entrances often serve this purpose. Methods of obtaining data from nests which are very close together are described, as well as methods of making population estimates of bees by means of the Lincoln Index. The following observations on each bee are recommended to learn as much as possible of habits and caste differences: (1) size of ovaries, (2) number of enlarged ovarioles, (3) number and size of largest oocytes, (4) presence of sperm cells in spermatheca, (5) presence of pollen in gut, (6) length of wing or some other index of size, (7) amount of wing and mandibular wear. The pollen loads of bees entering a nest can be marked with powder of different colors. Subsequent examination of cell provisions shows how many foragers cooperated in provisioning a cell. Replacement of a part of a nest with a glass tube provides opportunities for study of activities inside of the nest.

Zusammenfassung.

Die vorliegende Arbeit, ein Nachtrag zu dem Artikel von LINSLEY *et al.* (1952), beschreibt Methoden für das Studium der sozialen *Halictidæ* und anderer Bienen. Das relative Alter der Bienen kann durch Bewertung der Abnutzung von Mandibeln und Flügeln geschätzt werden. Einzelne Bienen können durch schnell trocknende Farben gekennzeichnet werden.

Derart markierte Individuen werden mittels einer Glasröhre zurück in das Nest gebracht. Dauerhafter als Farben oder Lacke, welche sich oft abreiben, sind Markierungen mit Alkohol- oder Azetonlösungen von Methyl- oder Ethyl-Eosin an den Flügeln. Methoden zum Aufhalten von Bienen beim Verlassen des Nestes oder bei der Rückkehr sind hier beschrieben. Eine dieser Methoden, die der näheren Untersuchung von Farbmarkierungen dienen, ist das Stellen von Drahtnetztüten über den Nesteingang. Erwähnt werden auch Methoden zur Beobachtung von nah-beieinanderliegenden Nestern. Die Bevölkerungszahl kann mit Hilfe des Lincoln Indexes geschätzt werden. Wir empfehlen die folgenden Untersuchungen an jeder Biene um soviel als möglich über das Verhalten und die Kastenunterschiede zu lernen : (1) Größe der Eierstöcke, (2) Anzahl der vergrößerten Ovariolen, (3) Anzahl und Größe der größten Oocyten, (4) Vorhandensein von Spermien in der Samenblase, (5) Vorhandensein von Blütenstaub im Darm, (6) Flügellänge oder ein anderes Maß der allgemeinen Größe, (7) Grad der Flügel- und Mandibelabnutzung. Die Blütenstaublasten von Bienen können vor dem Betreten des Nestes mit Farbpulvern bestäubt werden. Darauf folgende Untersuchung der Verpflegungsmassen der einzelnen Zellen ergibt die Anzahl der Futtersammler, die eine einzelne Zelle mit Proviant versorgt haben. Der Ersatz eines Teils des Nestes durch eine Glasröhre gibt Gelegenheit zum Studium des Verhaltens innerhalb des Nestes.

Résumé.

Dans ce complément à une note de LINSLEY et ses collaborateurs, les auteurs décrivent des techniques qui peuvent être utilisées dans l'étude des *Halictidæ* sociaux ou d'autres Abeilles.

Les méthodes employées pour apprécier les âges relatifs des Abeilles comportent, entre autres, l'étude de l'usure mandibulaire et de l'usure alaire. On décrit le marquage des individus avec des peintures à séchage rapide. Les Abeilles marquées peuvent être replacées dans le nid à l'aide d'un tube en verre. Les peintures s'usent souvent ; on peut obtenir un marquage plus tenace en colorant les ailes avec une solution de méthyl ou d'éthyl éosine dans l'alcool ou l'acétone. On décrit des techniques permettant de diminuer la densité relative des Abeilles qui entrent dans le nid ou qui travaillent à l'intérieur, de façon à rendre les marques colorées plus facilement visibles. De petits écrans coniques en cire placés devant l'entrée du nid peuvent remplir cet office. On décrit des méthodes permettant d'obtenir des résultats sur des nids complètement clos et des méthodes d'estimation de populations par l'emploi de l'indice de Lincoln. De manière à recueillir le plus d'indications possible sur les habitudes des différentes castes, on préconise les observations suivantes : 1^o taille des ovaires ; 2^o nombre d'ovarioles dilatés ; 3^o nombre et taille des plus grands ovocytes ; 4^o présence de spermatozoïdes dans la spermathèque ;

5° présence de pollen dans le jabot ; 6° longueur des ailes ou quelque autre indice de taille ; 7° degré de l'usure mandibulaire ou alaire.

Les pelotes polliniques, des Abeilles entrant dans le nid peuvent être marquées au moyen de poudres de différentes couleurs. L'examen ultérieur des provisions contenues dans les cellules indique combien de butineuses coopèrent à l'approvisionnement d'une seule cellule. La substitution d'une paroi de verre à la paroi du nid permet l'étude directe des activités des Abeilles dans le nid.

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DIE TYPEN DER ISOPTERA-SAMMLUNG DES ZOOLOGISCHEN STAATSMUSEUMS UND ZOOLOGISCHEN MUSEUMS HAMBURG

von Herbert WEIDNER

Bei der Bearbeitung der Systematik einer Tiergruppe ist der Vergleich mit typischem Material oft unerlässlich, wenn man Klarheit über eine Art erhalten will. Leider ist die Möglichkeit dazu oft nicht vorhanden, weil sich nicht feststellen läßt, wo das typische Material aufbewahrt wird. Es liegt daher, besonders nachdem durch den letzten Krieg viele Sammlungen zerstört worden sind, ein dringendes Bedürfnis nach der Veröffentlichung von Typenverzeichnissen der einzelnen Sammlungen vor, wie sie ja auch schon für verschiedene Tiergruppen von einigen Museen hergestellt wurden. Für manche Termitenarten gibt bereits SNYDER in seinem Katalog den Aufbewahrungsort der Typen an. Doch sind seine Informationen, wenigstens was die im Hamburger Museum aufbewahrten Typen betrifft, sehr unvollständig. Daher soll nachfolgend eine Liste dieser Sammlung gegeben werden. Da die alten Autoren keine Holotypen ausgezeichnet haben, so sind alle aufgeführten Typen als Paratypoide im Sinn von R. RICHTER (Einführung in die zoologische Nomenklatur. Frankfurt, 1948, S. 41) zu betrachten, aus denen bei einer Revision der einzelnen Arten erst der Holotypus noch ausgewählt werden muß. Nur in den Fällen, wo den Autoren ein einziges Tier für die Beschreibung vorlag, ist dieses als Holotypus gekennzeichnet. In der Reihenfolge und Nomenklatur folge ich dem Katalog von SNYDER, ohne damit ein Werturteil über die Arten abgeben zu wollen. SNYDER selbst wird nur dann zitiert, wenn er Hamburg als Aufbewahrungsort der Type angibt.

Zum großen Teil wurden die Typen auf Grund von Hamburger Material aufgestellt. Die Arbeiten, die sich auf dieses beziehen, sind in dem dem Typenverzeichnis vorangestellten Literatur-Verzeichnis mit * gekennzeichnet. Aus dem den anderen Arbeiten zugrundeliegenden Material erhielt das Hamburger Museum einzelne Paratypoide oder „Kotypen“ alter Bezeichnung im Tausch. Die Artenzahlen hinter den mit * ausgezeichneten Arbeiten beziehen sich auf alle in der Arbeit erwähnten, im Hamburger Zoologischen Museum aufbewahrten Arten. In der Typenliste sind aber nur die *species novae* aufgeführt. Alle Termitennester wurden im Krieg zusammen mit dem Museumsgebäude vernichtet, nur die in Spiritus aufbewahrten Tiere wurden gerettet und sind jetzt wieder geordnet und aufgestellt.

**I. VERZEICHNIS SYSTEMATISCHER ARBEITEN UEBER ISOPTERA,
DIE IM ZOOLOGISCHEN STAATSMUSEUM UND ZOOLOGISCHEN
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- *1949. SNYDER (T. E.). — Catalog of the termites (Isoptera) of the world (*Smith. misc. coll.*, **112**, 1-490). 23 Arten.

2. VERZEICHNIS DER IM ZOOLOGISCHEN STAATSMUSEUM HAMBURG AUFBEWAHRTEN ISOPTERA — TYPEN NACH DEM STAND VOM 31. 12. 1954

KALOTERMITIDAE.

1. *Neotermes fletcheri* (K. et N. HOLMGREN, 1917).
S. 139 : *Calotermes (Neotermes) fletcheri*, Im., Sold. Indien : Coimbatore.
2. *Cryptotermes havilandi* (SJÖSTEDT).
SJÖSTEDT, 1898 a, S. 212 : *Calotermes domesticus*.
SJÖSTEDT, 1900, S. 43-45 : *Calotermes havilandi*, da *domesticus* praeoccupiert.

HODOTERMITIDAE.

3. *Hodotermes mossambicus* (HAGEN).
SJÖSTEDT, 1914 a, S. 73-75, Taf. II, Fig. 9 : *Hodotermes macrothorax*, Sold. SW.-Afrika : Okahandja.

RHINOTERMITIDAE.

4. *Coptotermes michaelseni* (SILVESTRI, 1909).
S. 293-295, Taf. XIX, Fig. 106-121. W.-Australien : Mundijong. Im., Sold. Arb.
5. *Prorhinotermes canalifrons* (SJÖSTEDT, 1904).
S. 47-48 : *Termes (?) canalifrons*, Sold. Madagaskar : Tamatave.
6. *Schedorhinotermes celebensis* (HOLMGREN, 1911 b).
S. 458 : *Rhinotermes (Schedorhinotermes) celebensis*, Im. Sumatra : Indrapure-Estati, Deli.
HOLMGREN, 1913 b, S. 85-86 : *R. (S.) celebensis*.
SNYDER, 1949, S. 90.
7. *Schedorhinotermes maximus* (HOLMGREN, 1913 b).
S. 81, Taf. II, Fig. 15 : *Rhinotermes (Macrorhinotermes) maximus*, Im. (Holotype). Borneo : Tandjong.
SNYDER, 1949, S. 94.
8. *Schedorhinotermes putorius* (SJÖSTEDT, 1896).
S. 298 : *Termes putorius*, Im. Kamerun : Kitta.

TERMITIDAE.

9. *Amitermes hartmeyeri* (SILVESTRI, 1909).
S. 299-300, Taf. XX, Fig. 147-153 : *Monodotermes Hartmeyeri*, Sold., Arb. W.-Australien : Day Dawn.
10. *Amitermes heterognathus* (SILVESTRI, 1909).
S. 301, Taf. XX, Fig. 157 : *Hamitermes (?) heterognathus*, Sold. W.-Australien : Serpentine. (Auf dem Determinationszettel als „Type“ bezeichnet, in der Veröffentlichung fehlt dieser Fundort und ist ersetzt durch Day Dawn.)
11. *Amitermes obeuntis* (SILVESTRI, 1909).
S. 301-303, Taf. XX, Fig. 158-171 : *Hamitermes obeuntis*, Königin, Sold., Arb. W.-Australien : Serpentine, Mundaring Weir.
12. *Amitermes perarmatus* (SILVESTRI, 1909).
S. 300-301, Taf. XIX, Fig. 143-146 : *Monodotermes perarmatus*, Sold. W.-Australien : Yalgoo.
13. *Eremotermes fletcheri* (K. u. N. HOLMGREN, 1917).
S. 167 : Im., Sold., Arb. Indien : Coimbatore.
14. *Microcerotermes (?) camerunensis* (SJÖSTEDT, 1899).
S. 37 : *Eutermes camerunensis*, Im. (Holotype). Kamerun. Die Stellung dieser Art in dieser Gattung ist unsicher. Ich ordne sie vorläufig hier ein, weil Sjöstedt 1900, S. 175 schreibt, daß sie mit *Microcerotermes sikorae* verwandt ist. Ihre endgültige Einordnung kann erst bei Vorhandensein von weiterem Material erfolgen.
15. *Microcerotermes distinctus* (SILVESTRI, 1909).
S. 303-304, Taf. XX, Fig. 175-181 : Sold., Arb. W.-Australien : Coolgardie.

- Die Angabe bei SNYDER (1949, S. 137), daß sich die Holotype im Nat. Hist. Stockholm befindet, beruht auf einem Irrtum. Dort befindet sich nur von MjöBERG gesammeltes u. bestimmtes Material (Brief v. R. MALAISE vom 17. 11. 53).
16. *Microcerotermes fuscotibialis* (SJÖSTEDT, 1896).
S. 298 : *Eutermes fuscotibialis*, Im. Kamerun : Bonge.
 17. *Trichotermes ducis* (SJÖSTEDT, 1914 b).
S. 91-92 : *Eutermes ducis*, Sold. (Holotype). Belg. Kongo : Kimunze.
 18. *Cubitermes duplex* (HOLMGREN, 1913).
S. 357 : *Mirotermes (Cubitermes) duplex*, Sold., Arb. Zululand.
 19. *Cubitermes zenkeri* (DESNEUX, 1904).
S. 148 : Im., Arb. Kamerun : Yaunda.
 20. *Procubitermes arboricola* (SJÖSTEDT, 1897).
S. 126 : *Eutermes arboricola*, Im. Kamerun : Bonge.
 21. *Procubitermes natalensis f. brevior* (HOLMGREN, 1913).
S. 357 : *Mirotermes (Cubitermes) natalensis f. brevior*, Im. Zululand.
 22. *Termes kraepelinii* (SILVESTRI, 1909).
S. 298, Taf. XIX, Fig. 133-142 : *Mirotermes Kraepelinii*, Sold., Arb. W.-Australien : Mundaring Weir.
 23. *Capritermes ceylonicus* (HOLMGREN, 1911).
S. 194, 204-205, Taf. II, Fig. Q : Sold., Arb. Ceylon : Paradenya.
 24. *Capritermes fletcheri* (K. u. N. HOLMGREN, 1917).
S. 169 : Sold., Arb. Indien : South Kanara. (Von HOLMGREN als Kotypen bezeichnet !)
 25. *Acanthotermes acanthothorax* (SJÖSTEDT, 1898).
S. 204 : *Termes acanthothorax*, Sold., Arb. Kamerun : Kitta.
 26. *Synacanthotermes heterodon* (SJÖSTEDT, 1899).
S. 38 : *Eutermes heterodon*, Sold., Arb. Kamerun : N'dian.
 27. *Macrotermes bellicosus* (SMEATHMAN).
GERSTACKER, 1891, S. 186 : *Termes falciger*, Sold., Arb. Ostafrika : Mbusini.
SJÖSTEDT, 1900, S. 100 : *Termes bellicosus*.
 28. *Macrotermes michaelsoni* (SJÖSTEDT, 1914 a).
S. 77-79, Taf. II, Fig. 1, 10 : *Termes (Termes) Michaelsoni*, Im., Sold., Arb. SW-Afrika : Okahandja.
SNYDER, 1949, S. 214.
 29. *Macrotermes natalensis* (SJÖSTEDT).
SJÖSTEDT, 1899, S. 34 : *Termes tumulicola*, Im. Gr. Popo (Togo).
 30. *Macrotermes vitrialatus* (SJÖSTEDT, 1899).
S. 34-35 : *Termes vitrialatus*, Im. (Holotype). Kongo.
SJÖSTEDT, 1900, S. 87-89, Taf. 2, Fig. F : *Termes vitrialatus*.
 31. *Odontotermes (Odontotermes) assmuthi* (HOLMGREN, 1913).
S. 112-113 : Sold., Arb. Indien : Pusa. (Von HOLMGREN als Kotypen bezeichnet.)
 32. *Odontotermes (Odontotermes) badius* (HAVILAND).
SJÖSTEDT, 1904, S. 56 : *Termes badius*, Im. (Morphotype). Transvaal.
 33. *Odontotermes (Odontotermes) bangalorensis* (HOLMGREN, 1913 a).
S. 105-109 : Im. Indien : Bangalore.
 34. *Odontotermes (Odontotermes) bellahunisensis* (K. u. N. HOLMGREN, 1917).
S. 150-151 : Im., Sold., Arb. Indien : Bellahuni.
 35. *Odontotermes (Odontotermes) fockianus* (SJÖSTEDT, 1914 a).
S. 81-82, Taf. II, Fig. 11, 12 : *Termes (Odontotermes) fockianus*, Sold., Arb. SW-Afrika : Okahandja.
SNYDER, 1949, S. 227.
 36. *Odontotermes (Odontotermes) formosanus* (SHIRAKI).
HOLMGREN, 1913 b, S. 115-116, Taf. IV, Fig. 12 : *Odontotermes sinensis*, Im., China : Canton, Futschau.
SNYDER, 1949, S. 228.

37. *Odontotermes (Odontotermes) indrapurensis* (HOLMGREN, 1913 b).
S. 138, Taf. IV, Fig. 18, Im. (Holotype). Sumatra : Indrapura Estate Tandjong.
SNYDER, 1949, S. 230.
38. *Odontotermes (Odontotermes) javanicus* (HOLMGREN, 1912).
S. 36, Abb. 14, Taf. II, Fig. 1 : Sold., Im. Java : Salak.
HOLMGREN, 1913 b, S. 133, Taf. V, Fig. 6 (Sold.).
SNYDER, 1949, S. 230.
39. *Odontotermes (Odontotermes) latialatus* (SJÖSTEDT, 1897 a).
S. 124 : *Termes latialatus*, Im. Kongo.
SJÖSTEDT, 1900, S. 118-119, Taf. II, Fig. D : *Termes latialatus*.
SNYDER, 1949, S. 232.
40. *Odontotermes (Odontotermes) malabricus* (K. u. N. HOLMGREN, 1917).
S. 155. : Sold., Arb. Indien : Malabar.
41. *Odontotermes (Odontotermes) microps* (SJÖSTEDT, 1899).
S. 35-36 : *Termes microps*, Im. O.-Afrika : Tanga. — 1900, S. 119-120, Taf. III, Fig. F 1.
SNYDER, 1949, S. 233.
42. *Odontotermes (Odontotermes) monodon* (GERSTAECKER, 1891).
S. 186 : *Termes monodon*, Sold., Arb. Mozambique : Quilimane.
SJÖSTEDT, 1900, S. 109-110, Taf. III, Fig. J : *Termes monodon*.
SNYDER, 1949, S. 234.
43. *Odontotermes (Odontotermes) obesus f. gurdaspurensis* (K. u. N. HOLMGREN, 1917).
S. 149 : *Odontotermes (Cyclotermes) obesus f. gurdaspurensis*, Im., Sold., Arb. Indien : Gurdaspur.
44. *Odontotermes (Odontotermes) palmquisti* (SJÖSTEDT, 1907).
S. 16 : *Termes Palmquisti*, Im. Kilimandjaro.
45. *Odontotermes (Odontotermes) parvidens* (K. u. N. HOLMGREN, 1917).
S. 154 : Sold., Arb. Indien : Ganhati. (Auf Determinationszettel von HOLMGREN als *Odontotermes microdens* bezeichnet, dieser Manuskriptname wurde später von ihm geändert.)
46. *Odontotermes (Odontotermes) rehobothensis* (SJÖSTEDT, 1914 a).
S. 82-84, Taf. II, Fig. 3 : *Termes (Odontotermes) rehobothensis*, Im. (Holotype). SW.-Afrika : Rehoboth.
47. *Odontotermes (Odontotermes) robustus* (SJÖSTEDT, 1924).
S. 490 : Sold., Arb. Franz. Kongo : Brazzaville.
48. *Odontotermes (Odontotermes) simplicidens* (SJÖSTEDT, 1899).
S. 36 : *Termes simplicidens*, Sold. Kamerun : Ekundu.
49. *Odontotermes (Odontotermes) sundaicus* (KEMNER).
HOLMGREN, 1913 b, S. 134, Pl. IV, Fig. 7 : *Odontotermes (Odontotermes) javanicus f. Buitenzorgi*, Im. Java : Buitenzorg.
SNYDER, 1949, S. 241.
50. *Odontotermes (Odontotermes) trågardi* (HOLMGREN, 1913).
S. 328 : Sold., Arb. Natal.
51. *Microtermes divellens* (SJÖSTEDT, 1904).
S. 94-95 : *Eutermes divellens*, Im. Madagaskar : Nossi-Bé.
52. *Microtermes obesi* (HOLMGREN).
K. u. N. HOLMGREN, 1917, S. 159 : *Microtermes obesi*, Im. (Autohyle). Indien : Pusa.
53. *Nasutitermes aquilinus* (HOLMGREN, 1910).
S. 286-289, Abb. 59 : *Eutermes aquilinus*, Im., Sold., Arb. Brasilien : Flußgebiet des Itapocu.
54. *Nasutitermes brevioculatus* (HOLMGREN, 1910).
S. 220-224, Abb. 12 : *Eutermes brevioculatus*, Im. Paraguay : Estancia postillon, Puerto Max am Rio Paraguay.

55. *Nasutitermes ceylonicus* (HOLMGREN, 1911).
S. 197, Taf. III, Fig. M : *Eutermes ceylonicus*, Sold., Arb. Ceylon : Paradenyia.
56. *Nasutitermes columbicus* (HOLMGREN, 1910).
S. 256 : *Eutermes guayanae f. columbicus*, Sold., Arb. Columbien.
SNYDER, 1949, S. 271.
- Nasutitermes corniger* (MOTSCHULSKY).
57. HOLMGREN, 1910, S. 210, 237, Abb. 24 : *Eutermes costaricensis*, Im., Sold., Arb. Costa Rica : Pacuarito.
58. HOLMGREN, 1910, S. 239-240, Abb. 26 : *Eutermes insularis*, Sold., Arb. Costa Rica : Great-Island.
59. HOLMGREN, 1910, S. 240 : *Eutermes insularis f. obscurus*, Sold., Arb. Costa Rica : Port Limon.
60. *Nasutitermes costalis* (HOLMGREN, 1910).
S. 293-294, Abb. 64 : *Eutermes costalis*, Im. (Holotype). Trinidad.
SNYDER, 1949, S. 272.
61. HOLMGREN, 1910, S. 234 : *Eutermes cayennae f. brevinasus*, Sold., Arb. Niederl. Guiana : Paramaribo.
62. HOLMGREN, 1910, S. 227-228, Abb. 18 : *Eutermes haitiensis*, Sold., Arb. Haiti.
63. HOLMGREN, 1910, S. 228 : *Eutermes haitiensis f. labus*, Sold. Haiti : Cap Haitien.
64. HOLMGREN, 1910, S. 236-237, Abb. 23 : *Eutermes sanchezi*, Sold. Haiti : Sanchez.
65. *Nasutitermes crassicornis* (K. u. N. HOLMGREN, 1917).
S. 162 : *Eutermes (Eutermes) crassicornis*, Sold., Arb. Indien : Anamalai Hills.
66. *Nasutitermes ecuadorianus* (HOLMGREN, 1910).
S. 241-242 : *Eutermes peruanus f. ecuadorianus*, Im., Sold., Arb. Ecuador : Babahoyo.
SNYDER, 1949, S. 274.
67. *Nasutitermes ehrhardti* (HOLMGREN, 1910).
S. 276-278, Abb. 52 b, c : *Eutermes rippertii f. Ehrhardti*, Sold., Arb. Brasilien : Flußgebiet des Itapocu.
SNYDER, 1949, S. 275.
68. *Nasutitermes fletcheri* (K. u. N. HOLMGREN, 1917).
S. 161 : *Eutermes (Eutermes) fletcheri*, Sold., Arb. Indien : Shevaroy Hills.
69. *Nasutitermes guayanae* (HOLMGREN, 1910).
S. 254-256, Abb. 36 : *Eutermes guayanae*, Sold., Arb. Surinam.
SNYDER, 1949, S. 279.
70. *Nasutitermes indicola* (K. u. N. HOLMGREN, 1917).
S. 161 : *Eutermes (Eutermes) indicola*, Sold., Arb. Indien : Anamalai Hills.
71. *Nasutitermes itapocuensis* (HOLMGREN, 1910).
S. 278-280, Abb. 53 : *Eutermes itapocuensis*, Im., Sold., Arb. Brasilien : Flußgebiet des Itapocu.
72. *Nasutitermes jaraguae* (HOLMGREN, 1910).
S. 268-269, Abb. 47 : *Eutermes Jaraguae*, Sold., Arb. Brasilien : Flußgebiet des Itapocu.
73. HOLMGREN, 1910, S. 270-271 : *Eutermes aurantiacus*, Sold., Arb. Brasilien : Flußgebiet des Itapocu.
SNYDER, 1949, S. 281.
74. *Nasutitermes javanicus* (HOLMGREN, 1913 b).
S. 175-176, Taf. VII, Fig. 16 : *Eutermes (Eutermes) javanicus*, Sold., Arb. Java : Tjompea.
75. *Nasutitermes maculiventris* (SjÖSTEDT, 1904).
S. 104-105 : *Eutermes maculiventris*, Sold., Arb. Gabun.
76. *Nasutitermes nigriceps* (HALDEMAN).
HOLMGREN, 1910, S. 262-263, Abb. 42 : *Eutermes acajutlae*, Im. Salvador : Acajutla.
SNYDER, 1949, S. 289.

77. HOLMGREN, 1910, S. 249-295, Abb. 65 : **Eutermes guatemalae**, Im. Guatemala : San José.
78. HOLMGREN, 1910, S. 266-167, Abb. 45 : **Eutermes pacificus**, Sold. Westküste von Süd- oder Zentralamerika.
79. HOLMGREN, 1910, S. 265-266, Abb. 44 : **Eutermes pilifrons**, Sold., Arb. Curacao. SNYDER, 1949, S. 290.
80. **Nasutitermes piliceps** (HOLMGREN, 1910).
S. 289-290, Abb. 60 : *Eutermes piliceps*, Sold., Arb. Paraguay : Estancia Postillon Puerto Max am Rio Paraguay.
SNYDER, 1949, S. 293.
81. **Nasutitermes proximus** (SILVESTRI).
HOLMGREN, 1910, S. 269-270, Abb. 48 : **Eutermes aurantiacoides**, Sold., Arb. Brasilien : Flußgebiet des Itapocu.
SNYDER, 1949, S. 294.
82. **Nasutitermes rippertii** (RAMBUR).
HOLMGREN, 1910, S. 290-291, Abb. 61 : **Eutermes bahamensis**, Sold. (Holotype). Bahamainseln : Neo Providence Island.
HOLMGREN, 1910, S. 291-292, Abb. 62 : *Eutermes cubanus*, Sold., Arb. Cuba.
83. **Nasutitermes salebrithorax** (SjÖSTEDT, 1904).
S. 89-90 : *Eutermes salebrithorax*, Im., Sold., Arb. Seychellen.
84. **Nasutitermes tipuanicus** (HOLMGREN, 1910).
S. 281 : *Eutermes tipuanicus*, Sold., Arb. Bolivien : Tipuani.
SNYDER, 1919, S. 299.
85. **Tumulitermes apiocephalus** (SILVESTRI, 1909).
S. 306-307, Taf. XXI, Fig. 196-200 : *Eutermes apiocephalus*, Sold., Arb., Nymph. SW.-Australien : Jarrahdale.
86. **Occasitermes occasus** (SILVESTRI, 1909).
S. 307-308, Taf. XXI, Fig. 203-220 : *Eutermes occasus*, Im., Sold., Arb. SW.-Australien : Collie.
87. **Bulbitermes kræpelini** (HOLMGREN, 1913 b).
S. 174, Taf. VII, Fig. 14 : *Eutermes (Eutermes) Kraepelini*, Sold., Arb. Singapore.
SNYDER, 1949, S. 308.
88. **Grallatotermes grallatoriformis** (K. u. N. HOLMGREN, 1917).
S. 163 : *Eutermes (Grallatotermes) grallatoriformis*, Sold., Arb. Indien : Anamalai Hills.
89. **Hospitalitermes lividiceps** (HOLMGREN, 1913 b).
S. 209-210, Taf. VII, Fig. 35 : *Eutermes (Hospitalitermes) lividiceps*, Sold. (Holotype). Borneo : Tandjong.
90. **Trinervitermes grootfonteinensis** (SjÖSTEDT, 1914 a).
S. 86-87, Taf. II, Fig. 2, 5 : *Eutermes grootfonteinensis*, Sold., Arb. SW.-Afrika : Grootfontein.
91. **Trinervitermes hentschelianus** (SjÖSTEDT, 1914 a).
S. 88, 90-91, Taf. II, Fig. 4, 7 : *Eutermes hentschelianus*, Sold., Arb. SW.-Afrika : Otjosondyombo.
SNYDER, 1949, S. 327.
92. **Trinervitermes occidentalis** (SjÖSTEDT, 1904).
S. 93-94 : *Eutermes occidentalis*, Im. Port. Guinea : Bissao.
93. **Trinervitermes posselensis** (SjÖSTEDT, 1914 b).
S. 94-95 : *Eutermes posselensis*, Sold., Arb. Franz. Kongo : Fort Possel.
94. **Trinervitermes rapulum** (SjÖSTEDT, 1904).
S. 99-101 : *Eutermes rapulum*, Sold., Arb. Usambara : Tanga.
95. **Trinervitermes schubotzianus** (SjÖSTEDT, 1914 b).
S. 93-94 : *Eutermes schubotzianus*, Sold. (Holotype und Paratypoiden), Arb. Franz. Kongo : Fort Crampel.

96. *Trinervitermes togoensis* (SJÖSTEDT, 1899).
S. 37 : *Eutermes togoensis*, Im. (Holotype). Togo : Ho.
SJÖSTEDT, 1900, S. 201-203 : *Eutermes togoensis*.
97. *Trinervitermes trinervius* (RAMBUR).
SJÖSTEDT, 1904, S. 91 : *Eutermes mobilis*, Im. Franz. Sudan : Alahina.
98. *Trinervitermes zuluensis* (HOLMGREN, 1913).
S. 340-343, 348, 350 : *Eutermes (Trivernitermes) dispar* f. *zuluensis*, Im., Sold.,
Arb. Zululand.
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A POLISTINE COLONY USURPED BY A FOREIGN QUEEN ⁽¹⁾ ECOLOGICAL STUDIES OF *POLISTES* WASPS, II

by

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During my field study on the polistine wasp, I observed that a single foundation female (queen) attacked a nest belonging to another queen of the same species, drove away the latter and *usurped* the whole colony with its workers. As far as I know, such a behavior has not yet been reported. This interesting case may throw a new light on the inter-colonial relationship in the social insect. This is the record of observation with some consideration on the behavior.

I wish to express here my heartfelt thanks to Dr. K. IMANISHI of the Kyoto University and to Prof. T. KIRA of the Osaka City University for their valuable suggestions and criticisms.

RECORD OF OBSERVATION

About the middle of April, 1953, I found three nest (*A*, *B*, and *C*) of *Polistes fadwigae* DALLA TORRE (2) on the board-fence of a house (fig. 1) (3). On the same part of the fence, there were a few traces of nesting, including a vacant nest of preceding year (*O*). But it was not certain whether the

TABLE 1. — Organization of nests (May, 18 1953)

| Nest | No. of Cells | No. of Eggs |
|------|--------------|-------------|
| A | 21 | 19 |
| B | 13 | 12 |
| C | 11 | 11 |

(1) A portion of this paper was presented on April 23, 1955, at the annual meeting of the Ecological Society of Japan, held at Kyoto, Japan.

(2) The species is commonly found in central and southern part of Japan (Honshû, Shikoku and Kyûshû, including small adjacent islands).

(3) In Minô-chô, Osaka Prefecture, Honshû.

queens of these three nests had been led to the place by their homing instinct or not. At the time of the discovery, all the colonies were in the stage of solitary queen, no workers being present. Table 1 shows the organization of the nests on May 18.

On the same day, I transferred *B*-nest close to *C*-nest in the hope of artificially inducing a combined nest. But afterwards *C*-queen cut off *B*-nest by her mandibles and let it fall down to the ground. At the time of the present observation, only two nests, *A* and *C*, remained on the fence.

At 11: 30 *a.m.*, July 15, I had just finished recording the organization of the two nests when another queen (*X*) appeared in sight (4). It was cloudless. The status of the nests on the day are summarized in Table 2.

TABLE 2. — Organization of nests (July 15, 1953)

| Nest | Cell | ♀ | ♂ | Egg | Larva | | | | | Cocoon |
|------|------|---|---|-----|-------|---|---|---|---|--------|
| | | | | | 1 | 2 | 3 | 4 | 5 | |
| A | 25 | 1 | 6 | 0 | 1 | 9 | 8 | 2 | 0 | 4 |
| C | 14 | 1 | 1 | 4 | 2 | 2 | 2 | 4 | 0 | 0 |

The first attack (X → A)

X-queen flew straight toward *A*-nest and rushed upon it keeping the posture of orientation-flight. At the time of the attack, *A*-queen and three workers were on the nest and the three other workers were going out. *A*-queen confronted the invader at the base of the shaft of comb, while the workers assumed the threatening posture on the front edge of the comb with wings opened and antennae erected. In spite of all these, *X* dashed upon the nest (fig. 1-1) and fighting was began. On the comb, two workers bit at *X* with their mandibles and drove her out of the nest. Leaving the nest, *X*-queen flew to the top of the fence and paused there cleaning herself (fig. 1-2).

The second attack (X → C)

After ten minutes rest, *X*-queen turned on *C*-nest with similar orientation-flight (fig. 1-3). In the nest *C*-queen and a single worker were present. Contrary to the case of the first attack, the worker remained on the shaft with raised wings, and the queen herself showed a remarkable threatening behavior on the front of comb. She raised her antennae and opened her wings, quickly trembling with audible noise. *X* could not reach the nest at all.

(4) Workers were easily distinguished from queens by the color and size of body as well as by the weariness of wing. The queens, *A*, *B* and *C* were discriminated by artificial marking I had made on them.

The third attack ($X \rightarrow A$)

Turning back from *C*-nest, *X*-queen directly attacked *A*-nest again (fig. 1-4). This time, orientation-flight was not observed. At once there occurred a severe struggle on the comb between two of the workers and *X*, who bit each others with mandibles. Finally *X* dropped to the ground grappling with one of the workers (fig. 1-5). As soon as they reached the ground two wasps parted, the worker returning back to the nest without

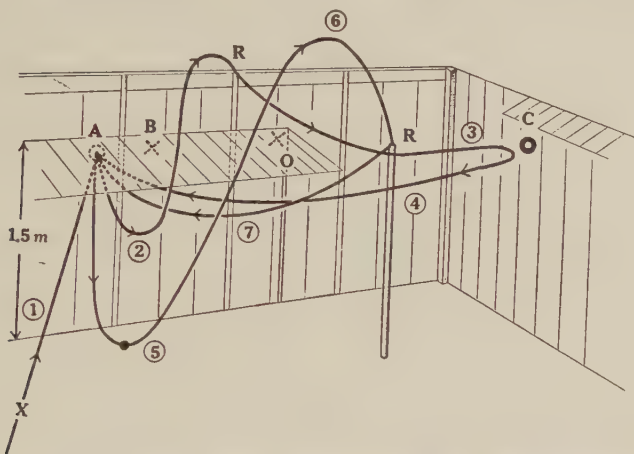


Fig. 1. — Sketch of the board-fence showing the situation of the nests and the course of attack. *A*, *B* and *O*: the nests under the pent roof. *B* was absent and *O* was vacant at the time of attack. *C*: the nest on the side of the fence. *R*: places where *X*-queen paused. 1-7: the course of attack.

delay. *X*-queen went for rest to the top of a pole standing nearby (fig. 1-6). Cleaning behavior was again observed there.

The fourth attack ($X \rightarrow A$)

Soon began the last attack to *A*-nest. *X*-queen, rushing straightfoward to the nest, directly bit at *A*-queen without paying any attention to the workers (fig. 1-7) and drove her out from the nest. Once driven out, she promptly flew away over the fence and never returned. Struggle between *X* and the workers immediately followed. Among the latter, younger workers were less aggressive and appeared less experienced in fighting. So the eldest one was the sole adversary against the invader. She bit a hind leg of *X*-queen, who in turn snapped her neck over the head. The fight continued for about three minutes in the same condition. During the time the two other workers moved around on the comb without trying to attack *X*.

At last the fighting worker became quiet, seemingly defeated. *X*-queen then released her and began to snap the younger workers one by one on their neck, who obeyed the foreign queen calmly without resistance. At this time one of the workers, who had been absent during the attacks,

came back to the nest and induced a little trouble among workers. The nature of the trouble was not clear for me. But it soon settled, when the newly returned worker was similarly snapped on the neck by X-queen.

TABLE 3. — Organization of nests (from July 22 to Aug. 19, 1953)

| Nest | Date | Cell | ♀ | ♂ | Egg | Larva | | | | | Cocoon |
|------|---------|-----------|---|----|-----|-------|---|----|---|---|--------|
| | | | | | | 1 | 2 | 3 | 4 | 5 | |
| A | July 22 | 24 | 1 | 6 | 0 | 0 | 2 | 10 | 6 | 2 | 4 |
| | 29 | 30 | 1 | 8 | 4 | 0 | 0 | 9 | 9 | 2 | 2 |
| | Aug. 12 | 32 | 1 | 10 | 6 | 0 | 0 | 9 | 7 | 4 | 2 |
| | 19 | 32 | 1 | 10 | 8 | 2 | 0 | 5 | 8 | 6 | 3 |
| C | July 22 | 14 | 1 | 1 | 3 | 1 | 1 | 3 | 4 | 0 | 0 |
| | 29 | 14 | 1 | 1 | 0 | 1 | 1 | 2 | 4 | 1 | 0 |
| | Aug. 12 | 14 | 1 | 1 | 0 | 1 | 1 | 2 | 2 | 0 | 0 |
| | 19 | Evacuated | | | | | | | | | |

The rest of the workers were also successively treated in the same way as they came home one by one. The invader had thus established the control over the whole colony.

Subsequent development of both A- and C-colony is shown in Table 3. As seen in the table, C-nest was evacuated half-way, while A-nest successfully developed under the new queen. Neither the expelled queen A nor B who had lost her nest appeared until the end of the season.

DISCUSSION

The earlier part of X-queen's life history is unknown. But judging from the date of the observations, she must have been nesting elsewhere in the neighborhood before the attack took place. Further, it is surmised that her own nest had been evacuated by some unknown causes, which led her to the unusual behavior described above.

On the nest evacuation in Japanese polistine wasps, I have reported in detail in the previous paper (1954). The evacuation was very frequent during the period before the eclosion of workers when a single female was founding her nest alone. Once the social or superindividual (5) stage had

(5) Superindividual stage. A term after Imanishi (1951). According to his opinion, so-called insect society is *not* the society in the true sense of the word, because none of its members is capable of independent life including both self-sustaining and breeding activities. Numerous sterile ergates in *insect societies* are nothing but the results of vegetative growth of a single queen which share various kinds of labor instead of herself. A whole colony, composed of a queen and many workers, is therefore homologous to an independent individual. He called such an organization as *superindividual organization* and discriminated it from *true social organization* which is an organized incorporation of independent individuals. The term is also entirely different from Wheeler's *superorganism*.

been reached, it became very rare. And it was concluded from the study that the later part of the solitary stage, with its highest frequency of evacuation, represented a critical period in the life history of polistine wasp, which can be overcome only through the establishment of the superindividual organization.

A remarkable contrast is found between *A*- and *C*-colony in the mode of their reaction against the attack of *X*-queen. In *A*-nest the workers were on the front of defence and it was after they had been defeated that *A*-queen joined in the fight against *X*. In *C*-nest, on the other hand, the queen herself took charge of the defence, while one worker was on the rear part of the nest. This contrast seems to be correlated with the difference in the degree of establishment of the superindividual organization in the two nests. As shown by Pardi (1947, 1948), all the members in a colony of superindividual stage are incorporated into a stable ranking organization. The behavior of *C*-colony suggests that the colony was not so well organized in this way that the queen herself forced to meet the invader. In *A*-colony, on the contrary, the queen was apparently quite dependent on the workers, which might be the result of the well established organization. The evacuation of *C*-nest soon after the attack (Table 3) seems to support the view.

The behavior of *X*-queen, tentatively named here *usurpation*, is essentially different from any other examples hitherto reported. I have reported a case that a queen of *Polistes antennalis* reconstructed her nest in another place after her first nest had been evacuated. According to Pardi, it is known in *Polistes gallicus* that a queen who has also failed to found her nest by herself, cooperates with another queen as an auxiliary female and that the nest building goes on polygynically. But either of the behaviors usually occur in the earlier part of the solitary stage. It may perhaps be impossible for a queen in so late a stage as in the present example to return to the nest-building activities against the normal course of her physiological development. Therefore the present type of behavior is considered most probable in a fecundated female of the superindividual stage.

This behavior also reminds us of the intraspecific fight for the occupation of nest (and of prey) observed in various species of solitary wasp (6). These cases are called *labor parasitism* because an individual (parasite) attacks another (host) to seize upon the results of the latter's labor in nest-building or prey-hunting. This labor parasitism and the present case have several features in common. But the former may cause a considerable degree of loss to the host but rarely leads to the extinction of it. On the contrary, however, for the expelled queen of the present observation, who has lost

(6) Examples of the *labor parasitism* in Japanese solitary wasps are as follows. Intraspecific « steal » of prey in *Batozonus annulatus* (Tsuneki 1935, 46); intraspecific steal and seizing of prey in *Anmophila infesta* (Tsuneki 1946); intraspecific steal of prey in *Episyron arrogans* (Shibuya 1937); intraspecific seizing of prey in *Pompilus reflexus* (Sakai 1932); intraspecific fight for the seizure of nest and prey in *Batozonus unifasciatus* (Iwata 1937 a); interspecific fight for prey betw. *Cryphonomyx dorsalis* and *Anoplius samariensis grandis* (Iwata 1937 b, 1947).

the results of her labor, there remains no other way than going to die. By this reason, the present case should not be regarded as a parasitic behavior. It is rather a mere competition between queens (or colonies). For X-queen herself, it is nothing but a compensation for the disturbance of her life cycle.

In the similar sense, it is by no means evolutionally related to *the social parasitism* reported in *Polistes perplexus* (Michener, 1951) and other polistine species in Europe (Richards, 1953). A clear distinction must be laid between mere competition and parasitic behaviors which result in the coexistence of both host and parasite. For the study of the evolutionary history of insect life, this distinction is very important and so-called labor and social parasitism should necessarily be reconsidered from such a point of view.

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II

NOUVELLES DE L'UNION

THE SECOND ANNUAL MEETING OF THE JAPANESE SECTION IN TOKYO (Oct. 17. 1954)

The Second Annual Meeting of the Japanese Section convened on Oct. 17. 1954 in the Library of the College of Medicine, Tokyo University. The Meeting was called to order by Prof. T. UCHIDA, President of the Japanese Section at 13. 40. There were present 15 members and 8 guests as follows:

Members: IMANISHI (K.), ISHIKAWA (R.), ITO (M.), KUWABARA (M.), MARUYAMA (K.), MORISITA (M.), OHGUSHI (R.), SAKAGAMI (S. F.), SHIDA (T.), TSUNEKI (K.), UÉNO (S.), UMESAO (T.), UCHIDA (T.), YAMANAKA (M.), YASUMATSU (K.).

Guests: FURUKAWA (H.), IIDA (M.), ITO (Y.), KITANO (H.), NAGASE (H.), NAKANISHI (T.), TANIGUCHI (S.), YAMAMOTO (S.) (Prof. FURUKAWA and Mrs. YAMAMOTO became the member of the Union at this meeting).

Chairman: Mr. SAKAGAMI, the Secretary of the Japanese Section.

Management: Mrs. SHIDA and MARUYAMA.

A. Business Meeting (13.45-14.35).

1. The Secretary reported briefly the general affairs during the year. The statutes of the Japanese Section was discussed. A plan of the statutes was read by Mr. OHGUSHI, the planner, and explained by Mr. SAKAGAMI in each item. Some opinions were announced successively by Dr. FURUKAWA, Dr. IMANISHI, Prof. KUWABARA, Dr. MORISITA, Mr. ITO and Dr. YASUMATSU. Thereafter, under the decision of the President, the most of the original plan was adopted unanimously with minor modifications. (The Statutes of the Japanese Section corresponds for the most part with those of the Union and operate completely under the latter.)

2. The Secretary demanded for members the quick sending of the cotisation of the Union. The cotisation for the Japanese Section was fixed, for the time being, as 40 yens. Moreover, the Secretary demanded the sending of the papers written by the members or their abstracts as an important obligation of members.

3. It was agreed that, until the next meeting in Fukuoka, the Secretariat of the Section is situated also for 1955 in the Zoological Institute, Faculty of Science, Hokkaido University, Sapporo under the management of the present membership (Prof. UCHIDA: the President, Mr. SAKAGAMI: the Secretary and Treasurer). However, the distribution of the members is so concentrated near Kyôto and Tokyo, that Messers OHGUSHI (Kyôto) and MARUYAMA (Tokyo) admitted to help the Secretariat in various practical ways.

B. *Photographing* (14.40: At the Entrance of the College of Medicine).

C. *Lectures* (15.00-18.45) (Prof. UCHIDA and Prof. FURUKAWA absent).

1. SHIDA (T.), **The Life of a common wasp, *Vespula lewisii*** (Cameron).

Based upon the results of numerous field observations on *Vespula lewisii*, some problems common to the social wasps were discussed in the following order: Biology of the hibernated females, differentiation of the habits in corresponding to the development of the nest, the causal factors for the development of workers, trophallaxis and habits of males. The most remarkable phenomena are the occurrence of robber wasps among the post-hibernating females just as in the honeybee and the resulted tendency to the social parasitism.

Discussions betw. the lecturer and Dr. IMANISHI, Dr. MORISITA, Prof. KUWABARA, Prof. TSUNEKI, Mr. SAKAGAMI and Mr. YAMANAKA.

2. ITO (M.), **Fundamental properties of social insects from the standpoint of comparative sociology, with special reference to the interactions among certain "non-social" insects.**

The fundamental importance of the group effect by the schools of ALLEE and GRASSÉ and its future availability on the studies of the so-called social insects were discussed with special reference to the social facilitation and the ecological origin of the sociality. The basic concept of the group effect lies on the optimal density in both the individual and group levels. The cooperative and disoperative interactions may be evoke below or above the optimal density. The higher degree of the optimal density may correspond to that of the sociality. But, ALLEE's optimal density bears in itself two weak points: 1. The unstability of the operational standard in comparing various populations differing in species, stage, environment, etc. 2. The unidirectional assertion of the importance of the higher densities as a measure of the sociality.

Therefore, it seems to be preferable, that more objective standards are selected for the future investigations (for ex. UTIDA's space of iso-effect of density or *eco-density*). Even to the insects regarded ordinarily as "non-social", the group effect gives an influence which leads the subjects towards the loss of self-perpetuation as an individual and the resulted

double phases in life modes, being comparable to the division of labour and group integration among Hymenoptera and Isoptera.

Finally, three levels of socialization under the intraspecific competition were proposed hypothetically: 1. The equivalent-harmfulness for more or less all the constituents. 2. Establishment of the non-equivalency among constituents due to the dominance order. 3. Occurrence of the complementary heterovalency among individuals based upon the loss of individuality by the caste-differentiation.

Active discussions were made around the problem of the sociality between the lecturer and Mr. SAKAGAMI, Mr. ITO (Y.), Dr. MORISITA, Dr. IMANISHI, Prof. KUWABARA.

3. MORISITA (M.), **On the sociality and individuality among animals.**

Owing to the too vivid discussions around the above two lectures, there was already no sufficient time for Dr. MORISITA. He promised, therefore, the detailed lecture in the next meeting (1955 in Fukuoka) and summarized briefly the above two lectures and suggested several important sides on the sociality and individuality of animals.

Discussions betw. Dr. MORISITA and Dr. IMANISHI, Mr. IIDA.

D. *Dinner* (18.45-20.00, at the Gakushi-Kaikan, Tokyo Univ.).

The following persons were present:

IMANISHI, ISHIKAWA, ITO (M.), KUWABARA, MARUYAMA, OHGUSHI, SAKAGAMI, SHIDA, TSUNEKI, UÉNO, YAMAMOTO, YAMANAKA, YASUMATSU.



The rear row (from left to right).

Mr. Nagase, Mrs. Yamamoto, Mr. Ishikawa, Miss Nakanishi, Mr. Ohgushi, Mr. Maruyama, Mr. Sakagami, Miss Taniguchi, Mr. Itô (M.), Mr. Kitano, Mr. Umesao, Mr. Shida, Mr. Itô (Y.), Mr. Iida.

The front row (from left to right).

Dr. Yasumatsu, Dr. Imanishi, Dr. Morisita, professor Uchida, professor Furukawa, professor Kuwabara, Mr. Yamanaka.

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It is difficult to summarize here shortly IMANISHI's huge system of speculation based upon the plenty of experience during his life-course as a field investigator. On the level of ecosystem his theory sharply opposed to all the community doctorines which postulate various enclosed systems. Apprehending typologically all the ecological groupings, he brings a theory of open system based upon the habitat segregation among synusia and compound synusia.

Furthermore, he criticizes ALLEE's works on the aggregation, especially his unidirectional accentuation of beneficial effects alone. If the gregarious life is an aspect of sociality, the solitary life mode must be another important aspect. Whether gregarious or not, the society is defined by him as follows: A field in which the group formation is possible or not, namely the field in which a species live spatially and temporally irrespective of gregarious or not. His *society* starts therefore from the species-society, *specia*. He proposes *specion* as the basic unit of *specia*. This means an organic unit as the carrier of both the individual—and species—maintaining capacities, and therefore corresponds ordinarily to each individual except such cases as sessile colonies of marine invertebrates and so-called social insects. In the latter cases, only the co-existence of reproductive and non-reproductive forms make possible to maintain the life, consequently only the set of these two forms is equivalent to each ordinary female of non-social insects. Therefore, the unit (*specion*) of the society (*specia*) is here not each individual but a kind of superindividual aggregate. True social phenomena among so-called social insects is limited only to the relationship among such superindividuals. Numerous suggestive opinions are included in the above papers. (He proposed the *genia* and *genion* for the social insects instead of *specia-specion* but not published his opinion.) (Sh. F. SAKAGAMI.)

1954. MARUYAMA (M.). — **Adenosinetriphosphate content and apyrase activity during metamorphosis of the wasps, *Vespula lewisii*** (*J. Fac. Sci. Tokyo Univ., Sect. IV. Zool.*, 7, 61).

1. ATP content in the whole body of *Vespula lewisii* decreases gradually during pupation, imaginal differentiation, and early adult life. 2. Apyrase activity of the whole brei undergoes an alteration corresponding with muscle development. 3. Acid and alkaline phosphatase activities are much lower than the apyrase activity in the adults.

1954. MORIMOTO (R.). — **On the nest development of *Polistes chinensis antennalis*** Pérez. I. (**Studies on the social Hymenoptera of Japan III**) (*Sci. Bull. Fac. Agric., Kyushu Univ.*, 14, 337, in Jap. with English resumé). 1. A founding female makes 30-40 cells in the solitary period, the mode of enlarging the nest depends highly on the nest-site. 2. Oviposition ceases for some days after the hatching of the first larva. The younger larvae (to 3. instar) are fed only by fluids, the older ones by both fluids and flesh. 3. 5-10 workers emerge under the care of founding female alone. After their emergence, the mother concentrates her task to brood-care and oviposition. If she dies, the ovipositing workers increase. The development of nests stops when the males begin to appear. — 1954. **On the nest development of — II (Studies — IV)** (*Ibid.*, 14, 511, in Jap. with English resumé). — 1. There is a direct relation between the duration of the incubation period and the number of cells made by a founding female. Moreover, the environ. conditions, esp. the temperature influence markedly the enlargement of nest. 2. Ovip. rate of founding females increase when the larvae reach 4-5 instar. Such older larvae are fed with protein-rich food, a part of which is also taken by female and results the increase of oviposition. 3. Ovip. rate of founding females increases after the cocooning of larvae in the nests under the warmer condition but not in those under cooler one. This may be explained by the decreased amount of labour due to the decreased breeding activity and the lower body temperature. 4. After the appearance of workers, the ovip. rate of founding female increases gradually and, corresponding with the periodical emergence of workers, the ovip. rate also fluctuates periodically. 5. Ovip. rate of the founding female is independent of the number of empty cells. 1954. **On the development of — III. Relation between the removal of eggs and larvae from the nest and the oviposition of the founding female (Studies — V)** (*Ibid.*, 14, 523, in Jap. with English resumé). — 1. Emergence of newly hatched larvae as the limiting factor to the rate of ovip. and cell construction of the founding

female was again ascertained. The ovip. rate does not increase by the partial removal of eggs and larvae, i. e. by the increase of empty cells. 2. The females tend to deposit the eggs to cell-walls facing to comb centre, probably due to (a) their natural attitude in the earlier life that they grasp the entrance of the cells when ovipositing, and (b) the tendency of females to deposit intensively into the empty cells at the central area of comb rather than those of the outer rings. 3. The disappearance of eggs is highly correlated with the hatching of the young in the other cells. It can be explained from the fact that the young larvae are fed often with comparatively newly laid eggs attached to the cell-walls of the peripheral area of comb.

1950. MORISITA (M.). — **Migration and population density of a water-strider, *Gerris lacustris* L.** (*Contrib. from the Zool. Inst., College of Sci., Kyoto Univ.*, No. 65, 149, 149 pp., in Japanese). The structure of the surface-film community composed of supraneustons was discussed with special reference to the habitat segregation among several species of water-striders. The process of density fluctuation in aggregations of *Gerris lacustris* was analysed at several small pools. From the occurrence of various density types and the observation of marked individuals, it was confirmed that the density fluctuation in each aggregation is heavily influenced by those of neighbouring ones and consequently by the frequent immigration and emigration among aggregations. Due to the continuous immigration, the spatial size as well as the density of each aggregation increases but only to the maximal extent of about 2 m in diameter. Beyond this limit, the aggregation maintains its extent and density by the emigration. The tendency of such a self-maintenance caused by the self-limitation of individual movement was proved statistically not by the ordinary quadrat method, but by the significant deviation from the formula of random movement by spacing method: $P = \frac{a(2l - a)}{l^2}$ (P: Probability in

which the spatial displacement of a marked individual in two successive observations lies in the arbitrary length of a , l : the maximal length along which the strider can displace), or later in Postscript, $P = \frac{a^2}{l^4} (\pi l^2 - \frac{8}{3} al + \frac{1}{2} a^2)$, ($a \leq \frac{l}{2}$, l : the length

of one side of a square). Thus the size and density of aggregation is self-regulated and self-equilibrated in relation with those of the neighbouring ones by the balance of immigration and emigration. — 1952. **Habitat preference and evaluation of environment of an animal. Experimental studies on the population density of an ant-lion, *Glenuroides japonicus* M'L.** (*Ecol. & Physiol.*, 5, 1, — in Jap. with English resumé). — The strong tendency of the ant-lion to prefer the fine sand to the coarse one for pit-formation falls with the increasing density. Therefore, the values of habitats themselves can be expressed by the population density as *environmental density*. For instance, if the probability that the first individual settles in the fine sand is larger than $\frac{1}{2}$, while the second one settles in the same part with the probability of $\frac{1}{2}$, we can consider that, for the habitat preference of the animal, value of the fine sand having one individual in it is as same as that of the coarse sand without individuals: namely, $E_B - E_A = 1$ (E_B & E_A is the environmental values of the fine and coarse sands expressed by the pop. density, namely *environmental density*).

Assuming the probability settles an individual in the fine sand is $\frac{E_B + D_B}{E_A + E_B + D_A + D_B}$ (D_B & D_A : Pop. density in the coarse and fine sand respectively), the probability that x individuals settle in the fine sand when $n + 1$ individuals are introduced into the experiment-box is calculated by the following formula:

$$Px(n + 1) = \left(\frac{E_A + x/s}{E_A + E_B + n/s} \right) Px(n) + \left(1 - \frac{E_A + (x - 1)/s}{E_A + E_B + n/s} \right) Px-1(n)$$

where s = area of the fine sand = (in his case) area of the coarse sand. The

frequency distribution of the observation coincides well with the expected value by the formula. The theory of environmental density may be applicable for the studies on the population density of other animals. — 1954. **Dispersion and population pressure. Experim. studies on the pop. density of an ant-lion.** — II (*Jap. J. Ecol.*, **4**, 71, in Jap. with English resumé).—Released in the centre of a field, the increase of the rate of dispersion in normal larvae is proportional to that of the initial numbers of larvae exist in the field, and is expressed by $y = N(l - e^{-(b+c/N)^S})$ (y : Indiv. number found in the field with extent of s ; N : Initial individual number, b & c : constant).

Indices P , α & β were proposed to indicate respectively the degree of the pop. pressure, the barrier effect to the spatial distribution and the velocity of distribution. By using these indices the relation betw. the pop. densities and the rate of dispersion were analysed mathematically. Moreover, by comparing the values of P of three spp. of insects, it was shown that the pop. pressure/unit area is largest in the ant-lion, smallest in the rice-weevil, while intermediate in the azuki-bean weevil when the pop. densities are equal to one another.

1954. OHGUSHI (R.).—**On the plasticity of the nesting habit of a hunting wasp, *Pemphredon lethifer fabricii* Müller** (*Mem. Coll. Sci., Univ. Kyoto, Ser. B*, **21**, 45).—The partition between each cell in a nest is often omitted. The fullgrown larvae are found occasionally in the same space without cannibalism. Moreover, the mother-daughter contact can be seen in some nests. These facts seem to suggest the dawn of a social relationship.

1954. SAKAGAMI (S.).—**Ueber einige Hummelarten von Hokkaido u. Kurilen Inseln** (*Systematische Studien der Hummeln. V*, Kontyu, **21**, 84).—*B. terrestris japonicus* aus Kurilen Inseln, *B. hypnorum calidus* aus Hokkaido u. Kurilen neu berichtet. Beschreibung von *B. tersatus* Smith mit *B. t. kurilensis* ssp. nov.

1947. TAKAMATSU (Y.).—**On the structure of the reproductive organ and the genitalia of *Vespula lewisii* (Cameron) (Hym., Vespidae) (Seibutu, 2, 166, in Japanese).**—General description of the mentioned organs in both sexes, including difference betw. reproductive females and workers. 1949. **On the post-embryonic development of the genitalia of *Vespula lewisii* (Cameron) (Seibutu, 4, 161, in Japanese).**—The distinction of sex in the abdominal end can be possible when the larvae reached to 3.5 mm in length. Through the continuous observation of the post-embryonic development in the later stages, it was confirmed that the genitalia of both sexes originate from both the tergites and sternites.

1949. UMESAO (T.).—**Social interference between individuals, its concept and experiments** (*Biol. Sci.*, **1**, 19, in Japanese).—The criticism of the current trends of sociology as a branch of biology. Instead of the generally adopted opposition of more or less arbitrarily defined "group" versus individual, the construction of objective and deductive sociology was proposed basing on the interaction among individuals. Defining the soc. interaction based upon the difference of behaviour when other individuals co-exist or not, the quantitative determination of the interaction was experimented with tadpoles in the field of probability. The +, — and 0 interaction was quantitatively determined by the difference of the distribution of individuals from the randomized theoretical value. The method employed allows its application to various organisms and phenomena as a useful tool constructing a more objective sociology.

1928. YAMANAKA (M.).—**On the male of a paper wasp, *Polistes fadwigae* Dalla Torre** (*Sci. Rep. Tôhoku Imp. Univ., Ser. Biol.*, **3**, 256).—Short notes on the parthenogenetic production of males by both the nest mother and virgin workers.

1954. YOSHIKAWA (K.).—**Ecological studies of *Polistes* wasps, 1. On the nest evacuation** (*J. Inst. Polytechn., Osaka City Univ.*, 5, 9).—Observing the development of nests of *Polistes antennalis* & *P. fadwigae*, the nest evacuation was confirmed in 90 % of the total 69 queens in a limited area, and mostly before the eclosion of workers. Evacuation in the social stage was represented only by a single nest of *P. antennalis*. Discussing the causal factors of evacuation, it was concluded that the later part of solitary stage represents the most unstable period throughout the developmental process of the nests.
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NOTES ET ANALYSES

1954. BRIAN (A. D.). — **The foraging of bumble bees** (*Bee World*, **35**, 61-67, 81-91). — A review of the subject dealing with: the senses of bumble bees (*Bombus*) in relation to foraging; the behaviour of and factors influencing foragers in the field and in the nest; type of flowers visited, tongue length of different species, corolla biting, constancy and economic importance of bumble bees.
1954. VOWLES (D. M.). — **The orientation of ants. I. The substitution of stimuli** (*J. Exp. Biol.*, **31**, 341-355). — Von Frisch has shown that in the honey-bee orientation established in relation to one directional stimulus (light) can be transferred to another directional stimulus (gravity or polarized light). In the present work the orientation of ants has been studied in experiments in which one type of directional stimulus has been replaced by another. Light, gravity and polarized light have been used as stimuli. When light and gravity are interchanged, the ant's successive orientations to the two stimuli are correlated. The angle between the track and the stimulus is the same for both orientations. When light and polarized light are interchanged, the ant's successive orientations are again correlated. The actual relationship depends of the experimental conditions. When polarized light and gravity are interchanged there is no significant correlation between successive orientations. It is suggested that in bees and ants there is a single taxis mechanism for orientation to light, polarized light and gravity, and that the 'setting' of this mechanism during an orientation to one stimulus persists and partially determines the subsequent orientation to another stimulus.
1954. VOWLES (D. M.). — **The orientation of ants. II. Orientation to light, gravity and polarized light** (*J. Exp. Biol.*, **31**, 356-375). — The orientation of ants to gravity has been investigated, and it is shown that orientations symmetrically placed on either side of the vertical are confused. The georeceptor is located in the antenna, and is probably Johnston's organ. Only one antenna is in use at any one time during geo-orientation. The light compass reaction has been investigated and it is shown that orientations 0° and 180° are confused. No explanation can be offered for this. The results are discussed in relation to the hypothesis that ants have a taxis mechanism common to all senses. It is suggested that the function of this mechanism is to set up a temporary labile symmetry of the ant with respect to orientatory stimuli.
1955. VOWLES (D. M.). — **The foraging of ants** (*British J. Anim. Behaviour*, **3**, 1-13). — This is a comprehensive review of the foraging behaviour of ants and includes sections on: the stimuli releasing foraging behaviour; feeding behaviour and its releasers (collection of booty, collection of nectar, distribution of booty in the nest, regurgitation); individual differences in behaviour; the journey to and from the nest (visual, chemical, tactile, kinaesthetic, and other stimuli); and the influence of general environmental stimuli. A classification of foraging behaviour is proposed with a view to clarifying the problems involved.
1954. OCATON (W. G. H.). — (*Div. Entom., Pretoria*) *Veld Reclamation and Harvester Termite Control. Farming in South Africa*, **29**, (338) 243-248. — Illus. Overgrazing by sheep leads to further destruction by harvester Termites and much grassland degenerates to the inferior Karoo-bush land. Broadcasting chaffed hay poisoned with sodium fluosilicate brings surprising restoration of grassland, without report of any poisoning of stock on treated grounds.

A.-L. Pickens.

INFORMATIONS

TENTH INTERNATIONAL CONGRESS OF ENTOMOLOGY

Montreal, Canada, 1956

The Tenth International Congress of Entomology will be held in Montreal on August 17-25, 1956. Following the Congress a number of excursions to places of entomological interest will be arranged.

All those hoping to attend the Congress and wishing to obtain further information should communicate as soon as possible with the Secretary, Mr. J. A. Downes, Division of Entomology, Science Service Building, Ottawa, Ontario, Canada.

Le Dixième Congrès International d'Entomologie tiendra ses assises à Montréal du 17 au 25 août 1956. Des excursions susceptibles d'intéresser les entomologistes auront lieu après le Congrès.

Les personnes qui voudraient assister au Congrès et qui désirent recevoir des renseignements plus complets devront se mettre en rapport le plus tôt possible avec le secrétaire, M. J. A. Downes, Division of Entomology, Science Service Building, Ottawa, Ontario, Canada.

Der X. Internationale Entomologische Kongreß wird vom 17.—25. August 1956 in Montreal stattfinden. Im Anschluß an die Kongreßwoche werden Besichtigungen von entomologisch interessanten Plätzen durchgeführt.

Interessenten, die beabsichtigen, an diesem Kongreß teilzunehmen, werden gebeten, sich bezüglich näherer Einzelheiten so bald wie möglich mit dem Schriftführer, Mr. J. A. Downes, Division of Entomology, Science Service Building, Ottawa, Ontario, Canada.

El Décimo Congreso Internacional de Entomología tendrá lugar en Montreal del 17 al 25 de Agosto de 1956. A continuación del Congreso se organizarán una serie de excursiones a lugares de interés entomológico.

Las personas que deseen asistir al Congreso y quieran recibir una información más completa sobre el mismo deben ponerse en comunicación lo antes posible con el Secretario del mismo, Mr. J. A. Downes, Division of Entomology, Science Service Building, Ottawa, Ontario, Canada.

Published in France.

Le Gérant : GEORGES MASSON

Dépôt légal 1955 - 4^e trimestre - N^o d'ordre : 2140 - MASSON et C^{ie}, éditeurs, Paris

Imprimé par l'Imp. CRÉTÉ, à Corbeil-Essonnes (Seine-et-Oise), France.

Dépôt légal 1955 - 4^e trimestre - N^o d'ordre : 6452

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- 2° Les auteurs reçoivent gratuitement 50 tirés à part.
- 3° Les manuscrits doivent être adressés à l'un des membres du Comité de rédaction, qui les transmettra au secrétaire.
- 4° Les textes remis pour l'impression doivent être dactylographiés. Leur forme sera considérée comme définitive, et leur étendue ne pourra pas dépasser 20 pages dactylographiées (*), illustration comprise.
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- 7° Chaque article doit être accompagné d'un sommaire qui en résume les points essentiels. Il sera joint une traduction de ce sommaire en deux autres langues.
- 8° La disposition de la bibliographie doit être conforme aux règles suivantes de présentation :

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FEB 24 1956



Publication périodique trimestrielle.